THE FUNCTION OF 'REFERENTIAL' CALLS IN TWO FISSION-FUSION SPECIES: SPIDER MONKEYS (ATELES GEOFFROYI) AND CHIMPANZEES (PAN TROGLODYTES)

Patricia Teixidor

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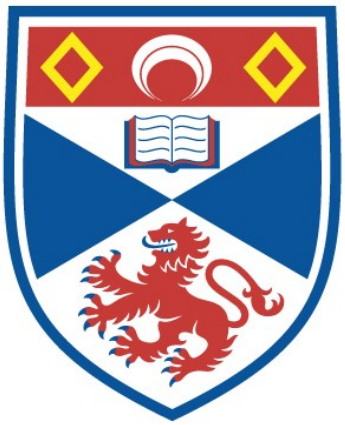

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The function of 'referential' calls in two fission-fusion species: spider monkeys (*Ateles geoffroyi*) and chimpanzees (*Pan troglodytes*)

by

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Dissertation submitted for the degree of Doctor of Philosophy
to the University of St Andrews, Scotland
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ABSTRACT

The problems of what primates communicate with their vocalizations and to what extent they refer to events in the external environment are raised in numerous studies of primate vocal communication. To investigate these issues, I concentrate on the calls of two primate species with a similar fission-fusion social organization. I report here the results of a one year field study on the Central American spider monkey (*Ateles geoffroyi frontatus*) and of a captive study on the chimpanzee (*Pan troglodytes*).

I collected observational data and conducted playback experiments on two types of calls of the spider monkey, *whinnies* and alarm *barks*. Spider monkeys use two functionally distinct *whinnies*, a feeding *whinny* and a locational *whinny*. Detailed acoustic analyses of *whinnies* given in different contexts showed that in three females an acoustic feature -number of arches in the fundamental frequency of the call- could be used to differentiate between them. Although the *whinnies* of different monkeys within the same community exhibit enough acoustical differences for individual vocal recognition to take place, spider monkeys did not discriminate familiar individuals' *whinnies* from those of strangers from another community. In predator contexts spider monkeys use *barks* to attract other conspecifics to a site. However, my data do not support the existence of two types of alarm *barks* for aerial versus terrestrial predators.

I conducted two different types of experiments on the calling behaviour of captive chimpanzees in response to food-finding. I examined whether the quantity and divisibility of food, or the presence of an audience, influence calling behaviour. Chimpanzees' food-associated calls, i.e. *rough grunts*, functioned to indicate food availability, and they were produced or suppressed depending on how shareable the food was and whether or not other individuals were nearby.

Several spider monkeys' and chimpanzees' calls have the ability to function referentially, but cannot be considered devoid of a motivational content.

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Chapter 1
INTRODUCTION

In this introductory chapter I present in the first place a review of the trajectory taken by the study of meaning in animal vocal communication, and a sketch of the theoretical framework on which my thesis will be based. Then, I examine cases of referential communication in two important types of signals for an individual's survival, those potentially referring to food and those potentially referring to danger (predators). An issue directly related to referential signalling is whether animals can communicate false information or withhold certain signals depending on the audience listening to it. I will briefly comment a few examples of vocal deception through signalling false information and through suppressing calls in certain social contexts; the latter has also been included under the topic of the 'audience effect'. Secondly, I introduce the two primate species on which I will focus throughout my thesis, spider monkeys (*Ateles geoffroyi*) and chimpanzees (*Pan troglodytes*), discussing the possible relation between their similar fission-fusion social system and several aspects of their vocal communication. As I do this, I will review various topics of primate vocal communication, whenever reported in either of the two primate species. Finally, a list of the few studies conducted on spider monkeys and chimpanzees' vocal communication, and a summary of the objectives I pursue in my thesis will end this introduction.

The study of meaning in primates and other animals' vocal communication

Until recently, studies of animal communication, whether by ethologists or behavioural ecologists, had generally ignored the causes of communicating. They focused instead on its evolutionary advantages, and avoided if possible any mention of unobservable terms such as intention or mental representation. Subsequently, studies of primate vocal communication have begun to change this focus (e.g. Seyfarth, Cheney and Marler 1980), by examining the issue of what information calls contain and to what extent primates have the ability to communicate about objects and events in their external world.

In the study of meaning in primate calls there have therefore been two alternative approaches (Marler, Evans and Hauser 1992). One is to assume that animal signals concern only information about the level of arousal or euphoria of the signaller, the so called affective or emotional hypothesis. According to this, animal signals lack the

capacity to function referentially, to encode information about objects and events independently of the speaker's motivational state (e.g. Smith 1977). Ethologists under this perspective have concentrated on the relationship between the signal produced, the environmental context, and the caller's motivational state (e.g. Eisenberg's 1976 study on spider monkey's, *Ateles fusciceps* vocal communication). The other approach is taken by some ethologists and psychologists who use a linguistic terminology to determine whether there is any analogy between the natural signals of animals and the words used in human language (e.g. Snowdon 1982). According to this perspective, some animals are able to transmit information about external events that is to some degree independent of their motivational state (Marler et al. 1992). Marler et al. (1992) proposed a useful model of referentiality and motivation to integrate the above perspectives. I will follow this model along several chapters for the interpretation of results. They propose that each term, motivational and referential, imply a model of the multidimensional relationship between the acoustic characteristics of signals (e.g. amplitude, duration, bandwidth), the properties of the classes of stimuli with which signals are associated (e.g. divisibility of a key food resource), and the motivational state at the time of signal production. For example, assuming that highly preferred foods elicit higher call rates, and that higher levels of arousal produce higher dominant frequencies, they describe a symbolic model of the way in which motivational and referential information might be reflected in the acoustic characteristics of a hypothetical food call (pp.76): if 'food characteristics and motivational state have independent effects on call structure, and the relationship between food characteristics and call rate is constant over a wide range of motivational state values (frequency), the signal is referential and ambiguity is minimal'. Furthermore, there is, according to these authors a continuum of signal classes in which, in one extreme, we have motivational signals determined entirely by the sender's motivational state and independent of stimulus characteristics; at the opposite end, referential signals, dependent exclusively on stimulus characteristics and unaffected by variation in motivational state. But most vocal signals would occupy intermediate positions on the continuum, having both referential and motivational components. Context will play a more crucial role in the process of decoding signals placed toward the motivational end of the continuum (Green and Marler 1979; Smith 1977), since contextual information functions to facilitate the selection of appropriate responses to 'motivational' signals (Marler et al. 1992).

Smith (1991) pointed out the risk of having a too narrow focus about external references and highlighted that animal vocalizations may have multiple referents:

i. several kinds of behaviours the caller is about to perform (e.g. Owings and Leger's 1980 study on the escape responses of California ground squirrels, *Spermophilus beecheyi;* in the predator context).

ii. Physical characteristics of a signaller (species, sex, or age; e.g. female macaques, *Macaca mulatta* identify their relative's calls when responding to recruitment screams, Gouzoules and Gouzoules 1984)
iii. External stimuli (type of food or predator; e.g. vervet monkeys', *Cercopithecus aethiops* alarm calls for different predators, Seyfarth et al. 1980).

I will briefly examine the existing evidence for referentiality in food calling and alarm calling in terms of the relationship between the signs and the things for which they stand, but not in terms of the mental representations of signaller and recipient. I am only interested here in what Seyfarth and Cheney (1993) defined as 'semanticity in the weakest sense', i.e. 'when an animal vocalization signals the presence of an external object or event, eliciting the same response as would its referent even when the referent itself is absent'. My study does not concern what they defined as 'semanticity in the strongest sense', i.e. 'when monkeys attribute mental states to one another, know that these mental states can affect behaviour, and as a result vocalize not only to influence what other animals do but also to influence what they think'. Only those studies which are relevant for future discussion of the results of this thesis will be reviewed.

Referential signalling in alarm calls

The first animal signals to be specified as referential were the alarm calls of the vervet monkey, studied by Cheney and Seyfarth (1990). Vervet monkeys in East Africa give acoustically different alarm calls to at least six different predators: leopards, several raptors and snakes (Struhsaker 1967). At least three of these alarm calls elicit a different, apparently adaptive response from other monkeys nearby (described in Seyfarth and Cheney 1993, p.197). When vervets are on the ground and they hear a leopard alarm from a conspecific, they run up into trees. Eagle alarm calls cause them to look up in the air or run into bushes; when the monkeys are in trees, eagle alarms often cause them to run out of trees and into bushes on the ground. Finally, snake alarms cause the monkeys to stand on their hind legs and peer into the grass around them. Through field experiments in which tape recordings of the three types of alarm calls were broadcast from hidden speakers, Seyfarth et al. (1980) proved that these vocalizations were sufficient to elicit adaptive, predator-specific escape responses, in the absence of real predators.

A central issue in the assessment of referentiality in animal signals is the 'production specificity' criterion (Macedonia & Evans 1993). Referential signals should exhibit a degree of stimulus specificity and therefore should not occur at appreciable rates in inappropriate contexts. The results of playback experiments with vervets show that on rare occasions, leopard alarms seem to be elicited by other types of predator. For example, Cheney & Seyfarth (1990) reported that leopard alarms were given at a low rate to eagles

and occasionally by vervets engaged in agonistic social interactions. These cases of 'inappropriate' leopard alarm usage are consistent with the idea that variation in affective state plays a more important role in the production of leopard alarms than in that of snake and eagle alarms, because these two latter call types do not appear to be produced in the absence of the predators with which they are normally associated (Macedonia & Evans 1993). Thus, the level of production specificity varies as a characteristic of each of the vervet alarm calls. Leopard alarms are less specific and hence might be placed further from the referential pole on a 'motivational-to-referential continuum' (Marler et al. 1992 above) than eagle and snake alarms.

In an extensive revision of the issue of meaning in mammalian alarm call systems, Macedonia & Evans (1993) compared the alarm calling behaviour of vervet, lemur and ground-dwelling sciurids vocalizations. They concluded that external reference plays a larger role in the alarm calls of vervet monkeys than in those of ground-dwelling scirurids (*Spermophilus beecheyi; S. beldingi*). Ground squirrel alarm calls do not denote different predator classes in the same way as some vervet alarms do, but instead reflect differences in response urgency perceived by the caller. The evolution of externally referential alarm calls may be expected to occur only in taxa where vocal differentiation of predator classes yields a significant advantage in reproductive success: apparently, in ground squirrels, it does not.

The same authors present a comparative study of the meaning of two species of lemurs' alarm calls, the ringtailed (*Lemur catta*) and the ruffed lemur (*Varecia variegata*). Both species respond with distinct alarm calls to aerial and terrestrial predators. The degree to which alarm calls of ringtailed lemurs and ruffed lemurs can be considered functionally referential are markedly different. In the ringtailed lemur alarms the eliciting conditions are specific, and playbacks are sufficient to evoke appropriate antipredator responses. In contrast, ruffed lemurs alarms have relatively low production specificity and do not elicit qualitatively different responses in playback experiments. Ruffed lemur alarms therefore do not qualify as functionally referential, although they are likely to provide receivers with a probabilistic estimate of predator type, particularly when contextual cues are available. Interestingly, the vocal antipredator behaviour of the ringtailed lemur resembles more closely that of the vervet monkey than it does that of the ruffed lemur. Ringtails and vervets have several highly specific alarm calls to which they respond in comparably specific ways, whereas the ruffed lemur's vocal responses to predators are less specific. Macedonia and Evans (1993) suggest a possible explanation for the evolution of externally referential antipredator calls, the incompatibility of responses required by different predator classes. Being relatively small-bodied, terrestrial, and living in an open habitat has increased predator pressure in ringtails and vervets over that of ruffed lemurs. Vervets and ringtails must respond to raptors and carnivores in two planes (ground and trees), and in ways that are frequently diametrically opposed.

However, this is not the case for ruffed lemurs, who have a highly arboreal lifestyle, reducing considerably the likelihood of facing a carnivore on the ground. In the case of ground-dwelling sciurids, responses to all types of predators occur on a single plane (the ground) where the burrow represents the primary retreat. An urgency-based alarm call system is thus adaptive for these mammals, whose response to different predator classes are qualitatively similar and require mainly information about the necessary speed of response.

Referential signalling in food calls

The possibility that food-associated calls provide evidence for referential signalling has been investigated in several primate and non-primate species: toque macaques, *Macaca sinica*, Dittus 1984; cotton-top tamarins, *Saguinus oedipus*, Elowson, Tannenbaum and Snowdon 1991; rhesus macaques, *Macaca mulatta*, Hauser and Marler, 1993a,b; domestic chicken, *Gallus domesticus*, Marler, Dufty and Pickert 1986a; Gyger and Marler 1988; common ravens, *Corvus corax*, Heinrich and Marzluff 1991. Dittus's (1984) study on the food calling behaviour of wild toque macaques in Sri Lanka showed that food calls were given by individuals when they encountered abundant and high-quality food. Individuals hearing the calls approached the caller and began to eat. Dittus argued that food calls have acquired signal value because they conveyed relevant information about feeding conditions to related group members. Food calls were not given when hunger level was supposedly greatest, i.e. in the morning, unless a rich food source was encountered. Thus, Dittus rejected an arousal interpretation of these calls. Toque macaques also emit these calls in other contexts, i.e. in response to the vocalizations of others, in response to the arrival of other group members, or when the sun appears after an overcast day (Dittus 1988). However, food calls in toque macaques might still fulfil the 'production specificity' criterion for external reference used by Macedonia and Evans (1993) because the majority of calls were given in the context of food. Thus, the production of these calls in the context of foraging seems enough to provide conspecifics with information about food but it is also likely that the calls are a manifestation of pleasure or excitement when finding warmth, companionship or food (Gouzoules et al. 1995).

Elowson et al. (1991) presented a critical review of some of the studies that have described food calls as referential signals, suggesting alternative explanations to the data supporting a representational hypothesis. They emphasized that it is important to know whether a call labelled as a 'food-call' is communicating about food alone or is communicating about courtship, excitement level or what behaviour the caller is going to do next. Their own study concentrated on whether the food-associated calls of cotton-top tamarins communicate an animal's preference for food or predict its subsequent

behaviour. They found that preference hierarchies for various foods differed greatly among animals and there was a positive correlation between the number of calls produced and the preference status of the food. Thus, *chirp* rate appeared to be related to an individual's own preference for a food item, and seemed to inform recipients of what specific action the caller will take with food, with rate of calling as an indicator of the strength of an animal's interest in a food. These results suggested that cotton-top tamarins use their calls to communicate honestly about their own food preferences.

Hauser and Marler (1993a,b) studied rhesus macaques's food-associated calls in the island of Cayo Santiago, Puerto Rico. They found five acoustically distinct calls. Two of them, *coos* and *grunts*, were given in both food and non-food contexts. The other three, *warbles*, *harmonic arches* and *chirps*, were only given to highly preferred foods. They found that the rate of producing food-associated calls was highest from hungry animals who had discovered a high quality food source and lowest from satiated ones finding chow (a low quality food). They suggested that rhesus macaques' food-associated calls are honest signals, 'announcing' food possession or ownership. Food calling monkeys received less aggression than did silent animals with food who were detected.

Marler et al. (1986a) showed evidence that cockerels' food calls function in a representational fashion. Cockerels varied the rate and number of calls when presented with different quality foods. However, these supposedly food-associated calls were also given in non-food situations, specially when individuals were separated from companions and were seeking to re-establish contact. The authors did not think that this was evidence against a representational usage of the calls, but was instead a deceptive use of a signal that in 'honest' use represents food (e.g. cockerels' food calls when no edible object is present and the female is furthest from the male, Gyger and Marler 1988).

It seems that sometimes animals transmit information in an 'honest' way, whereas in other circumstances they use their calls 'deceptively'. The degree to which animals can deceive one another depends crucially on how recipients assess and classify signals according to their meaning, and the study of deception can reveal how animals categorize events in the world around them (Cheney and Seyfarth 1991).

Deception and the 'audience effect' in natural communication

Vocal communication takes both cooperative and competitive forms; in some situations communication has advantages for both the sender and receiver (e.g. honest signalling might evolve in cases of kin selection, when for example a female's food calling benefits her offspring by attracting it to a rich food source; Wiley 1983). In other cases, animal signals seem to provide inaccurate information and in this sense apparently function to

deceive other individuals (e.g. threat displays of many species of birds and mammals). The view of animal communication as a manipulation of the recipients' behaviour to the signaler's benefit was first suggested by Dawkins and Krebs in 1978 (Dawkins and Krebs 1978), and then in their revised version of manipulation and 'mind-reading' in 1984 (Krebs and Dawkins 1984).

Deception through signalling false information occurs when one individual actively falsifies the information it conveys to another. An animal may occasionally falsify vocal signals by giving calls in inappropiate contexts, for instance there is anecdotal evidence that vervet adult males give false alarm calls when no predators are present, during intergroup encounters. Such calls are highly effective because they invariably cause others to flee (Cheney & Seyfarth 1990). There is also evidence that chimpanzees sometimes give loud *barks* when there is no visible threat nearby to distract the attention of another individual and thus gain access to a goal (e.g. an estrous female; reported in the Byrne and Whiten's 1990 tactical deception database, record #218, observer: Frans de Waal). The ability to modify and falsify signals is not restricted to primates. There is evidence that signal falsification may be quite common in birds. Alarm calls seem particularly appropriate for use in deception because receivers of the signal will frequently act prior to evidence of the veracity of the alarm since the risks implied in not responding is too large. Two studies have shown that sometimes birds give alarm calls when no predator is present, and are thus able to increase their food intake by driving away competitors, sometimes more dominant individuals, from concentrated food sources (Munn 1986, neotropical flycatching birds; Moller 1988, great tits). However, a common problem in these studies is the high proportion of 'false' alarm calls when no predator at all was present.

Signal falsification may also occur in food calling contexts. Gyger & Marler (1988) studied pairs of domestic chickens under semi-naturalistic conditions, concentrating on the hypothesis that the call refers to an edible object and can be used deceptively. The results showed that of all calling, 45% occurred when no identifiable object was present. Calls given by the male when no edible object was present occurred when the female was significantly further from the male than when food was present. The strongest argument against the deception hypothesis is the fact that calling without food made up such a high proportion of so-called food-calling events in the study. Although it is generally accepted that for deception to succeed dishonest use must be a relatively rare event, little is known about the precise limits involved, and the extent to which they may vary with the particular situation. In the previous study, the cost to a deceived female of responding to non-food calling will be low, and the benefits of intermittent access to a preferred food may be very high.

Deception of a different sort may take place when animals suppress their calling in situations in which they may gain some advantage by doing so, i.e. avoid feeding competition. Evidence of this type of deception has been found in vervet monkeys: adult males gave more alarm calls if they were with a female than if they were with another male, Cheney and Seyfarth 1985; rhesus macaques: individuals suppressed food-associated calls, Hauser and Marler 1993b; pygmy chimpanzees (*Pan paniscus*): discoverers of preferred food gave less calls in a social situation than when artificially isolated in a captive setting from all group members, in which there was no risk of losing any food, Van Krunkelsven et al. 1996. This type of deception may also fall into the category of what has been called the 'audience effect'. In chimpanzees, the evidence of call suppression is common (defined as 'concealment by silence' in Byrne and Whiten's 1990 database), e.g. chimpanzees suppressing loud calls or screams when 'patrolling' the boundaries of the territory or hunting (records: #192 by Boesh, and #193 by Goodall); individuals remaining silent when discovering small amounts of food (Wrangham 1975; Hauser and Wrangham 1987; Hauser et al. 1993). A typical case also described in chimpanzees is that females supressed copulation calls when mating with low ranking individuals (Tutin 1979). Hauser (1990) showed that in the wild female chimpanzees give copulation calls significantly more often when they are mating with older and higher ranking males, than when they are mating with younger and lower ranking males. In the absence of information about the function of copulation calls or the mechanisms underlying their production (Hamilton and Arrowood 1978), it is reasonable to assume that the conditions that typically cause a female to call are the same for old and young males, but that the costs and benefits of calling differ between males of different age or rank. Because females who suppress their copulatory calls often display the facial expressions accompanying call production, it seems likely that at least some of the necessary conditions for voluntary signal suppression have been met. In spider monkeys there is only one case reported by Milton in provisioned spider monkeys at Barro Colorado (Panamá) of what was defined as 'concealment by hiding and silence' (record #25 in Byrne and Whiten 1990). An adult male travelled in the ground (an unusual behaviour for this species) following a female who was travelling in the trees and when they were far away from other conspecifics, copulated with her for 30 min. Since mating is already very secretive in this species (Symington 1987) and copulation calls have not been reported, it is not clear to me how this example could represent a deceptive act by 'silence'. The behaviour of the male walking in the ground might be explained because in times of water scarcity spider monkeys exceptionally come to the ground to drink from waterholes. On the other hand, according to Symington (1987), opportunistic matings such as has been described for chimpanzees and woolly spider monkeys (Milton 1985) have never been observed for *Ateles* in free-ranging conditions.

The phenomenon of withholding certain information has also been studied under the label of 'the audience effect'. There is enough evidence in the literature demonstrating that, when an animal is in the presence of a signal referent (e.g. appreciated food item), there is an ability to modulate signal production according to the appropiateness of the caller's social circumstances. A large amount of work on this effect has been done with domestic chickens, revised in a comprehensive paper by Marler, Karakashian and Gyger (1991). In one of the studies reviewed, Marler, Dufty and Pickert (1986b) conducted experiments to determine whether a cockerel's food calling is affected by the presence and nature of an audience. The results showed that males gave food calls in the presence of strange and familiar females but completely withheld their calling in the presence of another male. Their conclusion was that a cockerel tendency to utter food calls when presented with food of a certain quality is strongly affected by the presence and nature of the receiver. In contrast with alarm calling (Karakashian, Gyger and Marler 1988), there is a difference in the effectiveness of a familiar female (mate) and a strange female to elicit the male's calling. This difference is stronger when we compare male responses to a 'strong' and a 'weak' food referent. With a preferred food, there is no difference in the amount of calling with a strange female and with the mate. However if something inedible is presented, the male hardly calls at all to his mate but calls at an appreciable rate to the strange female.

When considering the results of both alarm calling and food calling in cockerels, Marler et al. (1991) bring attention to the possibility that an audience influences signal production by changing the general arousal level of a signaler. They admit that arousal is an important phenomenon in animal behaviour and it does influence the occurrence of signal production in many circumstances.

An interesting aspect of the above reviewed topics, deception and the audience effect, is the possibility that their occurrence may reflect intentional and other cognitive abilities in animals (e.g. the ability to attribute knowledge to others, and to understand that other individuals' knowledge and beliefs may be different from their own). However, one always has to bear in mind that simpler mechanisms may be underlying these behaviours (e.g. the case of the audience effect could be reinterpreted in 'reflexive' terms, by multiplying the number of reflexes impinging on signal production, Marler et al. 1991).

Vocal communication of two fission-fusion species: spider monkeys and chimpanzees

In this section I will compare several aspects of the vocal communication of spider monkeys and chimpanzees, connecting them when possible with socio-ecological factors imposed by their fission-fusion social systems. As I go along I will briefly review several topics of vocal communication in primates (e.g. phonetic variation, individual variation, discrete versus graded signals, etc.) mentioning if they have been reported in these two and other fission-fusion species. Some of these topics will be retrieved and expanded in subsequent chapters of my thesis.

Similarities and differences in social organization

A fission-fusion society is characterized by individuals spending their time in small subgroups that frequently change size and composition. All the individuals in these subgroups are members of a single community (a number of animals that use the same range area and interact peacefully with one another; Chapman, Wrangham and Chapman 1995).

Several studies have emphasized the similarities in the social organization of spider monkeys and chimpanzees (van Roosmalen 1980; McFarland 1986; Symington 1987; Symington 1990; Fedigan and Baxter 1984; Chapman et al. 1995). Both chimpanzees and spider monkeys have a frugivorous diet with highly dispersed and seasonal food sources to which they seem to have adapted with a skillful knowledge of their availability (e.g. by monitoring the ripeness of its fruits and remembering economical routes between them), and a flexible social structure with mean subgroup size varying seasonally in relation to food supply (spider monkeys, van Roosmalen 1980; chimpanzees, Wrangham 1977). In both species adult individuals occupy 'core areas' within the community range, and male core areas are larger than female ones. Adult females range on their own more often than males and they emigrate between communitites. Male natal philopatry has been observed in both spider monkeys and chimpanzees (Symington 1987).

Some of the differences between the two species occur in the patterns of female receptivity and male mating strategies (e.g. in chimpanzees mating takes place openly, often accompanied by copulation calls, while in spider monkeys mating is always secretive; van Roosmalen 1980, Symington 1987), the strength of social bonds between males (e.g. less strong in spider monkeys than in chimpanzees; Symington 1987), and their different lifestyle, i.e. unlike chimpanzees, spider monkeys are completely arboreal.

Similarities in vocal communication

A recently published paper by Hohmann and Fruth (1995) has compared the vocal communication, particularly loud calls, of several primate species, to examine the relationship between vocal behaviour and social organization. To investigate whether interspecific differences in vocal behaviour reflect differences in the complexity of their social organization, they compared a large number of species having a 'harem group' social system (e.g. gorillas), with species having a fission-fusion social system (pygmy chimpanzees, spider monkeys, chimpanzees, and woolly spider monkeys, *Brachyteles aracnoides*). The most interesting result for present purposes is that they found a number of parallels in the vocal systems of fission-fusion species, e.g. both sexes usually give loud calls and use them for both intra- and inter-group communication, and several socio-ecological similarities as well, e.g. flexible spatial distribution, female biased adult sex ratio, female migration and low sexual dimorphism. Although their comparison of a larger number of species did not support an interrelation between type of social organization and sex differences in utilization of loud calls, their study represents an example of how to compare the vocal behaviour of different species with characteristics of their social organization.

Another similarity in the vocal behaviour of three fission-fusion species is that chimpanzees, spider monkeys and pygmy chimpanzees all produce calls when discovering an abundant food patch. Although there are minor sex differences in 'food call' production among common and pygmy chimpanzees, in spider monkeys females call at a rate 2.5 times that of males (Fedigan and Baxter 1984).

Characteristics of the vocal systems of spider monkeys and chimpanzees

One of the most common studied topics in primate vocal communication is that of the variability existing in the structure of primate calls (reviewed in Snowdon 1982; 1986; 1993). The first type of variability is the one Snowdon (1982), using a term from linguistics, described as 'phonetic' variability; that is, calls that superficially seem similar but are acoustically different and have different functions. The classical example of this phenomenon is the study conducted by Green with japanese macaques' *coos* (Green 1975). Besides showing correlations between calls with different structure and certain behaviours, several studies have also proved through playback experiments that individuals responded differently to different call variants (e.g. Pola and Snowdon 1975 with pygmy marmoset, *Cebuella pygmaea* trills). Eisenberg (1976) described calls similar

in structure but with identifible variants correlated with different functions in the spider monkey repertoire (e.g. *whinny* call). This type of variability has not yet been described in chimpanzees or in other fission-fusion species.

A different type of variability in primate calls is the one that indicates the identity of the individual caller, i.e. individual variability. In any social group of animals individuals might be able to identify one another by their vocalizations and responses might be different to different members of the group (Snowdon 1986, for revision). In primates with a fission-fusion social organization in which individuals spend large amounts of time separated from each other and each has the option of associating in subgroups of a different composition, the ability to identify one another's vocalizations will be most adaptive (e.g. for deciding whether to join a certain subgroup or not). Evidence of individual differences in the vocalizations of chimpanzees (*pant-hoots*) and spider monkeys (*whinnies*) has been found by Marler and Hobbett (1975) and Chapman and Weary (1990) respectively. In addition, Mitani and Brandt (1994) re-analysed inter-individual and within-individual acoustic variability in male *pant-hoots*. They found that *pant-hoots* vary less between individuals than within individuals. They explained the inter-individual similarity by suggesting that males who called together appear to match the acoustic characteristics of each other's *pant-hoots*. Thus, vocal similarities between males arise because these males spend considerable amount of time in association, engaged in chorusing behaviour. Moreover, they concluded that endogenous variables related to the emotional states of signallers and the same social factors mentioned above (i.e.association patterns), may serve as an important source of within-individual acoustical variation (e.g. males who chorused often with others produced more variable calls than individuals who chorused less often or called alone). No studies have investigated whether there are individual differences in the vocalizations of other fission-fusion species like pygmy chimpanzees or woolly spider monkeys.

Vocal structure variability between different populations of primates has been described in only a few cases of primate (reviewed in Snowdon 1986). In chimpanzees, Mitani et al. 1992 described subtle acoustic differences between the *pant-hoots* produced by males from the Mahale and Gombe populations (150km away from each other). Although the results were interpreted as evidence of dialectal variation which could implicate learning in the vocal acquisition process of chimpanzees, the amount of variability was small and the calls were recorded in different contexts. Results of a later study, Mitani and Brandt 1994, reinforced the conclusion that acoustic differences between members of the two populations were not large. No study has been conducted on this subject in spider monkeys or other fission-fusion species.

The environmental constraints imposed by the different habitats in which primates live may shape certain characteristics of their sounds to maximize detectability, resulting in variation in call structure due to sound localization (Snowdon 1986). Several studies have examined how sound is transmitted in different environments (Waser and Waser 1977; Brown 1982). They found that low-frequency sounds travel for a much longer distance than high-frequency sounds, and that in tropical forests high-frequency sounds are attenuated a greater extent. Thus, primates use long-distance calls in frequencies that can be transmitted over the greatest distances. Chimpanzees' long calls (Marler and Tenaza 1977) have sound frequencies falling within the window of least attenuation in a tropical environment, i.e. 500-2.500Hz (Waser and Waser 1977). Spider monkeys's long calls also exhibit average frequencies falling within this range (2.000Hz)(Eisenberg 1976). Eisenberg (1976) emphasized that in species that live in dense habitat where individuals are often out of sight from each other, i.e. spider monkeys, selection favours for highly frequency-modulated sounds. For example, during feeding it is important to produce a signal which can be heard by other group members to maintain cohesion wihin the group, thus spider monkeys produce highly-frequency modulated *whinnies* in this context.

When classifying the vocalizations of nonhuman primates in order to define their function, researchers have either described them as discrete or as graded signals, with the aim of determining whether a given species uses its calls in a categorical manner and how these categories are constituted (reviewed in Newman and Goedeking 1992). A call type may be discretely separated from other types. However, graded signals are those in which categories vary so much that different types become connectable by intermediate forms. Eisenberg (1976) defined spider monkey's vocal communication as a graded system in which vocalizations do not easily fall into discrete categories, but intergrade into one another. This author performed a motivational analysis of the spider monkey repertoire in which he showed how temporal patterning shifts in calls, for example *barks*, indicated a change in intensity of a given mood. Thus, there is according to him a series of calls associated with withdrawal and fear; a series of calls associated with friendly approach and a series of calls associated with attack, each exhibiting an intensity-graded series. The great majority of chimpanzee call types grade into one another through intermediates (Marler and Tenaza 1977). These authors found that the *waa bark* of chimpanzees was the most variable call of the repertoire, while four calls, i.e. *rough grunts*, *pant-hoots*, *coughs* and *laughter*, were the most discrete. The most graded and variable calls, e.g. *barks* and *screams*, may be also the most influenced by the emotional state of the caller. It has been thought since Darwin's writings (1872) that gradations in voice are the manifestation of graded changes in internal state (Newman and Goedeking 1992). Morton (1977) attempted to identify similarities in the relationship between emotional state and the acoustic features of vocalizations. He proposed 'motivational-structural (MS) rules' to

formalize the relationship between emotional state and acoustic structure. According to him birds and mammals use low frequency atonal vocalizations in highly aggressive situations, whereas they typically produce high frequency tonal vocalizations during non-aggressive or fearful situations. Hauser (1993), starting from the assumption that the fundamental frequency of a vocalization is negatively correlated with body weight, examined the relationship between body weight and frequency in a large sample of primate species. A second aim was testing Morton's MS rules. His results confirmed that larger species produce relatively lower-pitched vocalizations than smaller species, and provided support for some of the predictions discussed by Morton (1977; 1982). Vocalizations produced in the context of aggression tend to be low in frequency, whereas vocalizations produced in the context of fear tend to be high in frequency. This rule was true for common chimpanzee's calls but not for pygmy chimpanzees. Although no fearful calls were present in the spider monkey's call sample analyzed, their aggressive calls were all low frequency calls, confirming partly the above rule. There were no data for woolly spider monkeys. However, the other prediction in the MS rule was not proved, i.e. there was no relationship between motivational state and tonality. Hauser's explanation of this lack of complete support for MS rules is twofold: changes in motivational states may be associated with other acoustic variables not investigated in his study; for some primates the acoustic structure of the call is more closely related to the external referent (e.g. food, predator) than to the motivational state of the caller (mentioned in Marler et al. 1992).

In summary, there are a number of similarities between the vocal behaviour of chimpanzees and spider monkeys: the use of calls which advertise the discovery of food and attract other individuals to dispersed and patchy food resources (consisting mainly on ripe fruit); the use of long calls best adapted for transmission in tropical environments for inter- and intra-group communication; evidence in both species of individual vocal variability which suggests the existence of vocal recognition, although this has not yet been proved with playback experiments; and a vocal repertoire formed mostly by graded signals.

As we have seen above, chimpanzees and spider monkeys are also similar in their social organization. It has been proposed that these similarities are the result of convergent social evolution in response to similar selection pressures for obtaining safety from predators, obtaining access to mates and maximizing feeding efficiency (McFarland 1986, McFarland Symington 1988). However, few studies have concentrated on comparing the vocal communication systems of both species, on trying to correlate socio-ecological factors with vocal attributes (with the exception of Hohmann and Fruth's 1995 study), or investigating further similarities which could imply a convergent evolution in their vocal communication as well as in their social organization.

Previous studies of vocal communication in spider monkeys and chimpanzees

When I first started to review the literature on spider monkey vocal communication I was faced with a lack of studies focussing on any aspect of the vocal communication of this species. However, I was lucky that at least one study describing in detailed the vocal repertoire of this species had been conducted. Eisenberg (1976) provided a syntactic description of the vocalizations of captive black spider monkeys (*Ateles fusciceps*) and free-ranging Central American spider monkeys (*Ateles geoffroyi)*, together with a functional classification supported by a contextual description. Captive *Ateles geoffroyi* 's behaviour has also been studied by Eisenberg and Kuehn (1966) with a small section dedicated to vocalizations. Andrew (1963) presented some data on the vocalizations of *Ateles belzebuth.* Three dissertations have been conducted on free-ranging spider monkeys, focussing in different aspects of their ecology and social organization, including some section about vocal communication as well. Klein (1972) provided some data on vocal behaviour during intergroup encounters in *Ateles bezebuth.* Van Roosmalen (1980) studied habitat preferences, diet, feeding strategy and social organization in *Ateles paniscus*, refering briefly to their calling behaviour (mainly long calls). Symington (1987) studied ecological and social correlates of party size in *Ateles paniscus*, dedicating one chapter to the effect of predation in party size and the monkey's alarm calling behaviour in this context. More recently several papers on different aspects of the vocal communication of free-ranging *Ateles geoffroyi* have appeared (Chapman and Lefebvre 1990; Chapman and Weary 1990; Chapman et al.1990). The results of some of these studies will be reviewed in detail in the pertinent chapters.

The case of chimpanzee's vocal communication is somewhat different in that more research has been devoted to its study. The vocal repertoire of the chimpanzee has been studied extensively by Marler (1976), and Marler and Tenaza (1977) at Gombe National Park, Tanzania. Other studies focussing mainly on one type of call, i.e. *pant-hoots*, have been conducted at Mahale mountains, Tanzania by Mitani et al. (1993), in Kibale forest, Uganda by Hauser (1990), Clark (1991), Clark and Wrangham (1993; 1994), and in Gombe by Marler and Hobbett (1975). Other studies on chimpanzees' behaviour not focussing specifically on vocal communication but referring to it to some extent are Goodall's (1986) long term study in Gombe and Ghiglieri's (1984) in Kibale.

Aims and outline of thesis

When I first became interested in primates' vocal communication, the issue that most appealed to me was what information was transmitted in for example the loud calls of a chimpanzee male and what the calls were used for. In this thesis I examine the function and meaning of calls in two primate species, spider monkeys and chimpanzees. The first part of the thesis presents a field study of the vocal communication of spider monkeys located in Santa Rosa National Park, Costa Rica. The second part is an experimental study on the food calling behaviour of captive chimpanzees housed in Edinburgh Zoo, Scotland. Captive studies have the advantages of more controlled conditions and the possibility of manipulating social contexts and food forms to investigate specific factors affecting calling. The aim of this research is threefolded:

i. To increase our knowledge of spider monkey's vocal communication by concentrating on the following aspects:
- detailed acoustical description of a specific call, the *whinny*
- function and meaning of *whinnies*
- vocal discrimination of a specific call in the repertoire, i.e. familiar versus stranger's *whinnies*
- the use of alarm calls by spider monkeys

ii. To provide evidence on the issue of whether specific vocalizations of spider monkeys (i.e. the *whinny* and the *bark*) and chimpanzees (i.e.*rough grunts* and *pant-hoots*) refer to features of the physical environment.

iii. To investigate experimentally what social (e.g. rank) and ecological factors (e.g. food quantity) affect the production of food-associated calls in chimpanzees and whether they take into acount the social audience when calling.

I will briefly give an overview of the thesis and describe the chapters that follow. Part 1 presents a field study of spider monkeys, starting with Chapter 2, which describes the study site, general methods (e.g. habituation and identification of the monkeys), study subjects and specific methods used for the behavioural data collection. Chapter 3 consists on a brief summary of some aspects of feeding and ranging behaviour, presenting previous research together with my own findings as a way of introducing the next chapter. Chapter 4 presents quantitative analyses of the contexts in which *whinnies* are used, followed by playbacks experiments of two possible variants of the *whinny*, feeding versus locational. In Chapter 5, I present detailed acoustic analyses of the *whinny* call, focussing on its variation between individuals and contexts. Chapter 6 is a theoretical review on the issue of intergroup encounters and territoriality in fission-fusion species,

providing the reader with the necessary background for the next experimental chapter. Chapter 7 presents playback experiments to determine whether spider monkeys can discriminate familiar individuals versus stranger's *whinnies*. In Chapter 8, I examine the reaction of spider monkeys to the perceived threat of predation (through visual or auditive predator cues) as a first approximation to obtain more information on the issue of the species' anti-predator behaviour. In Chapter 9, I discussed all results of the first part of the thesis together. Then, the second part consists of Chapter 10, which is an experimental study on captive chimpanzee's food-associated calls, the effect of the social audience and the quantity/divisibility of food on their calling. Finally, Chapter 11, discusses conclusions about the possibility that chimpanzees and spider monkeys's use referential signals in their vocal communication.

Part 1. FIELD WORK ON SPIDER MONKEYS' VOCAL COMMUNICATION

Plate 1. Adult spider monkey female *Ateles geoffroyi frontatus* alarm barking.

Chapter 2
Study site and general methods

2.1. STUDY SITE

2.1.1. General

Costa Rica is located in Central America, bordering Nicaragua in the north, and Panama in the south. It has developed a national park system consisting of 15 national parks and 11 wildlife refuges and reserves, unparalleled by any other in Latin America. The national parks occupy a 15% of the country's territory.

Santa Rosa National Park (SRNP) was established in 1971. It is a 37.117-ha National Park, situated in the Guanacaste Province, 35km Northwest of the city of Liberia, between the Pacific Ocean (Gulf of Papagayo) and the Pan-American Highway, with geographical coordinates 10° 45' to 11° 00' N and 85° 30' to 85° 45' W (Janzen 1983)(see figure 2.1.). At present SRNP is part of the Guanacaste Conservation Area, major conservation project started by the ecologist Daniel Janzen. This focuses on the ecological and cultural restoration of the dry forest habitat, once widespread in Mesoamerica but today very much endangered (Janzen 1986). The Guanacaste Conservation Area includes the Guanacaste, Santa Rosa and Rincón de la Vieja National Parks, the Refugio de Vida Silvestre Isla Bolaños, the Estación Experimental Horizontes and the Area Recreativa Bahía Junquillal (see figure 2.2.). This 700 square kilometres conservation area comprises a wide range of different vegetation: all kinds of dry forest habitats, evergreen rain forests in the volcanoes, mangrove swamps along the coastal areas, and river-margin vegetation.

SRNP is situated on a plain with several plateaus. Topographically it may be divided in three parts: a high plateau, the lower valleys and some hills in between. Elevations range from 317 m to sea level (see figure 2.3.). According to the ecological map of Costa Rica (Tosi 1969), the upper plateau of Santa Rosa is classified as tropical premontane moist forest, warm transition, whereas there is a large band of dry forest, cool-moist transition, on the Pacific coast.

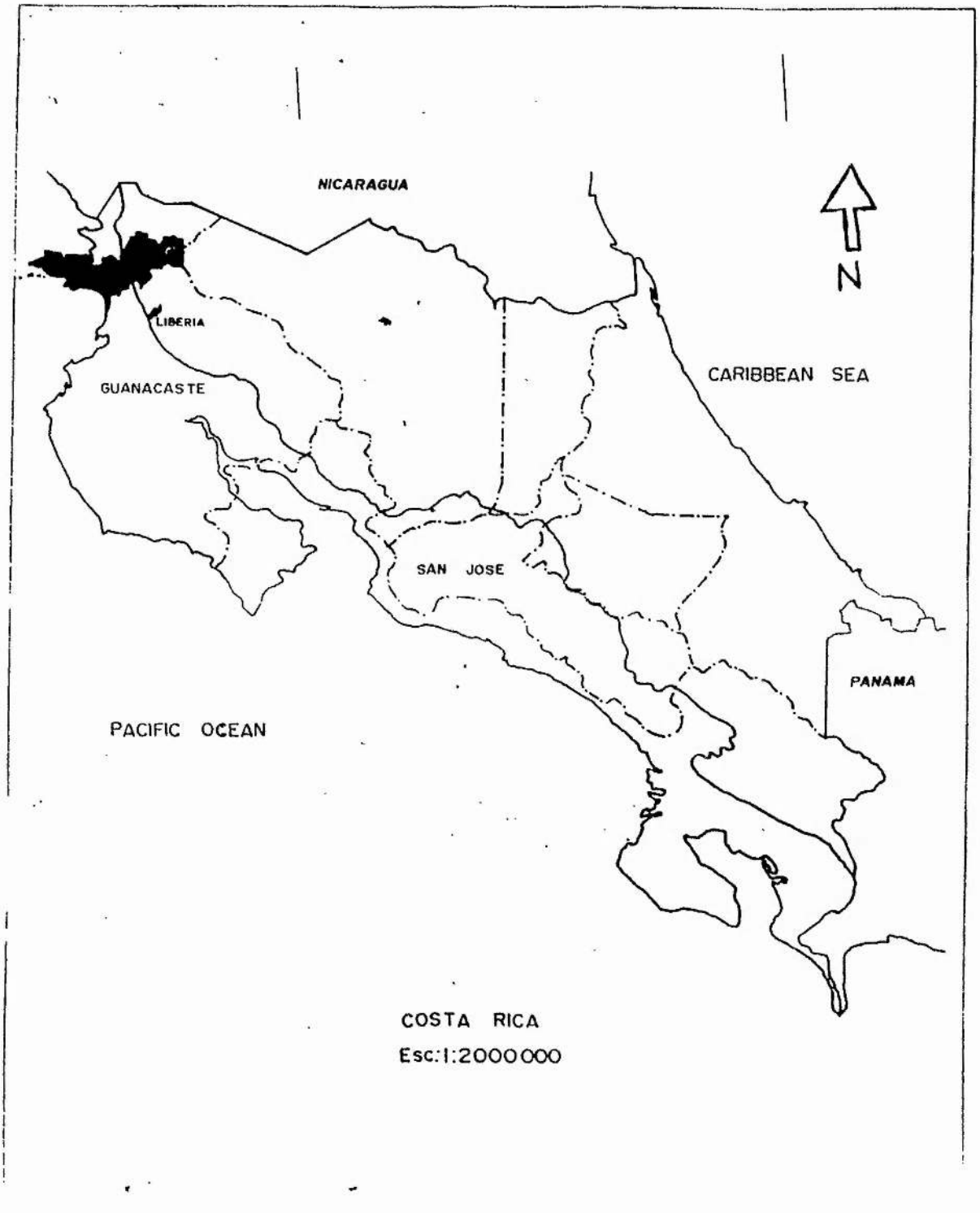


Figure 2.1. Location of Santa Rosa National Park in Northwestern Guanacaste Province, Costa Rica (adapted from Janzen 1986).

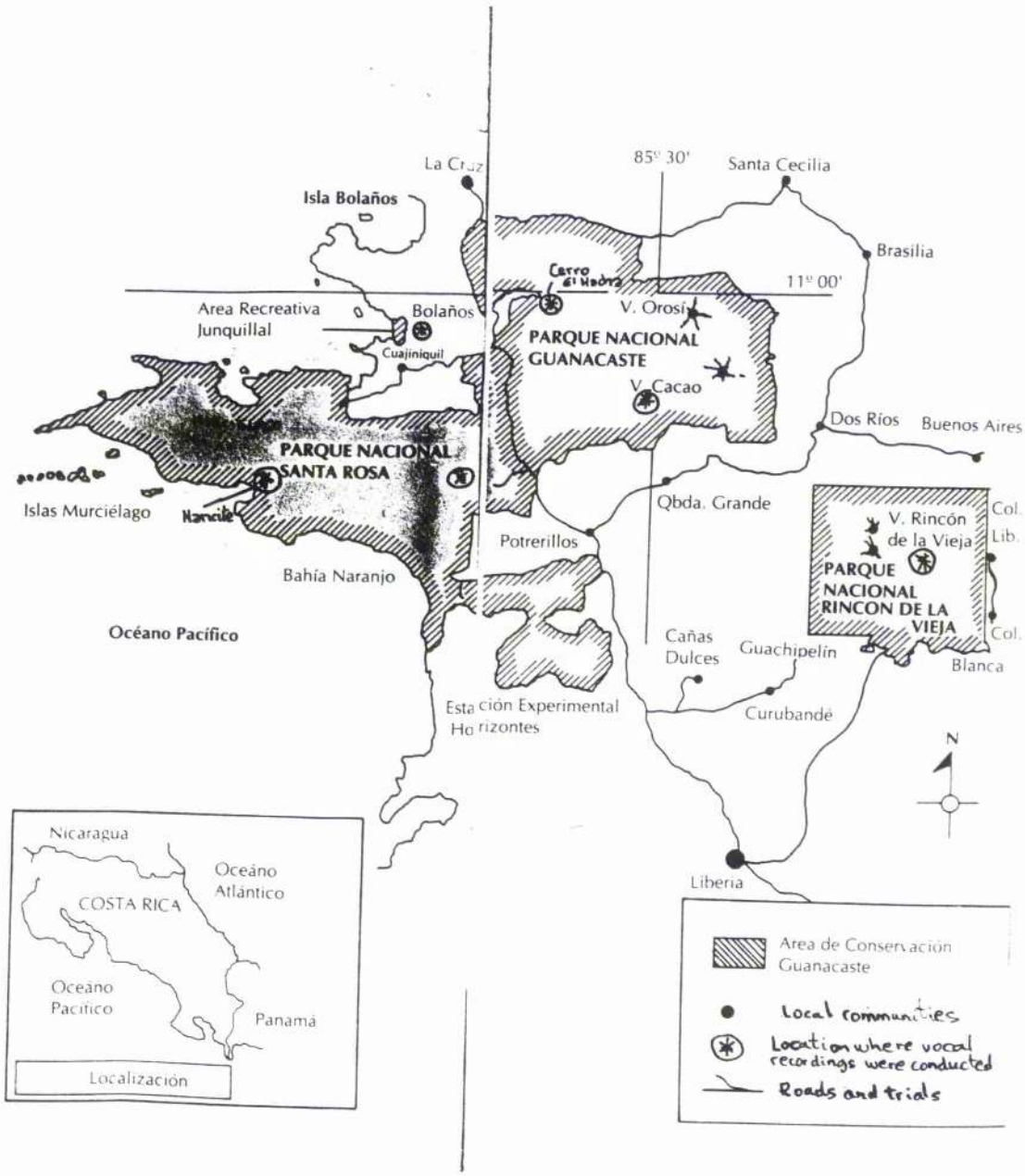


Figure 2.2. Map of the Guanacaste Conservation Area with the location of different sectors where vocal recordings of spider monkeys were conducted.

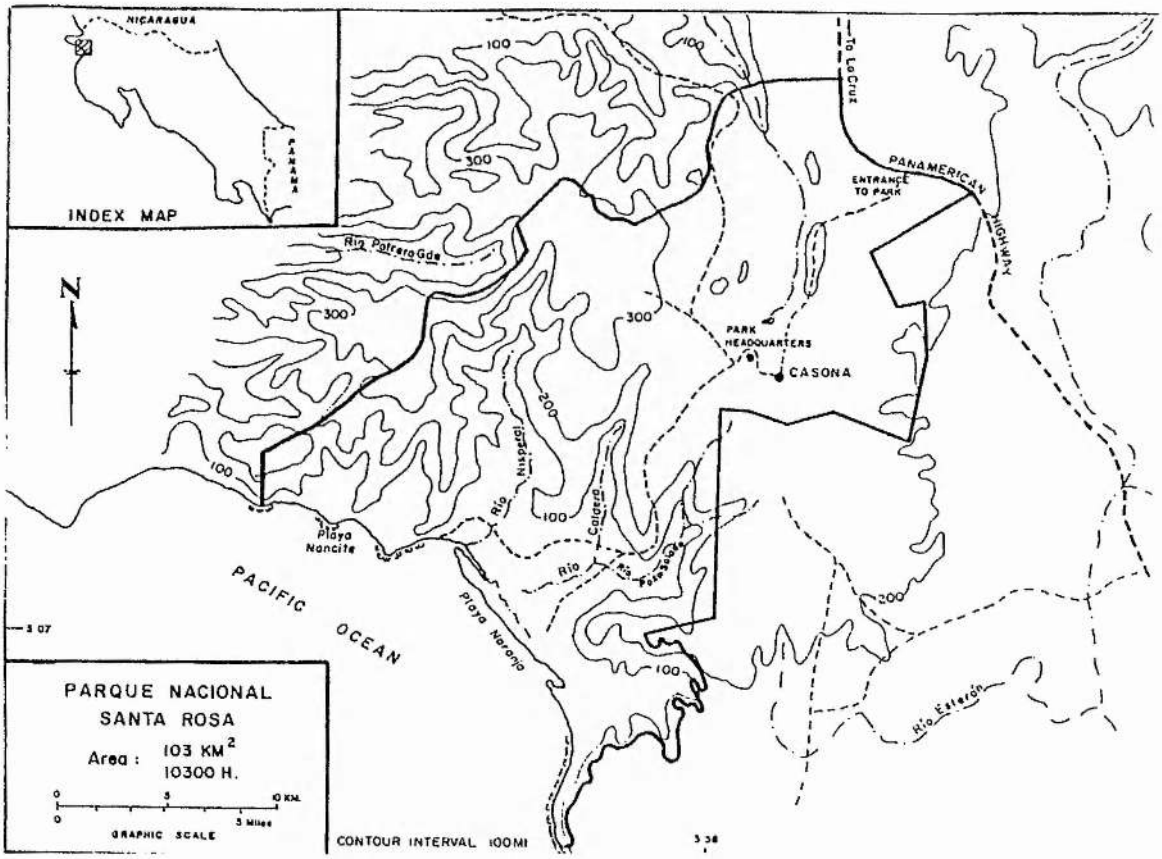


Figure 2.3. Map of Santa Rosa National Park (Tropical Science Center).

2.1.2. Climate

The average annual rainfall in SRNP varies from 900 mm to 1200 mm (see figure 2.4.) and the average annual temperature is 27°, with maximum temperatures of 40° in March and April and minimum of 16° in January and February. The most characteristic aspect of this climate is its seasonality, with a dry season beginning in mid-December and ending in late May, and a wet season extending to the rest of the year. The dry season is characterized by strong winds from the Northeast, the loss of leaves by deciduous trees and the absence of water in rivers and creeks. In Mesoamerica, the Pacific dry forest has the distinctive feature of receiving 900 to 2400 mm of annual rainfall during 5-7 months of the year and virtually no rain during the 5-7 month dry season (see figure 2.5., monthly rainfall at SRNP during the period 1982-91). It also has a short period of up to six weeks of dry season in the middle of the rainy season (July and August). Nocturnal low temperatures range from 16-23 C, and diurnal maxima from 26 to 38 C in most of the lowland dry forest habitats (Janzen 1986).

2.1.3. Habitat

More than 300 years ago large part of the forest which once constituted the upper plateau of Santa Rosa was cut down and altered by burning, grazing and farming. At present approximately 60% of the territory is covered with savannahs formed by pastures. The most common plant is the African pasture grass jaragua (*Hyparrhenia rufa*), introduced in 1921 when part of the area was used for intensive cattle. Among the most salient dry forest habitats that may be found in the park are (only those relevant for the primates present in the park will be explained with more detail, following Janzen 1986):

a) seasonal rivers and creeks: during the dry season there are waterholes and springs, remnant from the previous rainy season which constitute important water sources for animals and plants. The evergreen vegetation along the banks produces a cool and humid refuge. The watercourses and watercourse banks are a major natural habitat of water, shade, fruit, and animal prey for many mammals. There is, for example, a waterhole in the study area which contains a volume of about eight litres of water at any one time and is daily visited by several deer, five to fifteen coatis, five to fifteen peccaries, two to five agoutis, five to twenty white-faced monkeys, and numerous birds (Janzen 1983).

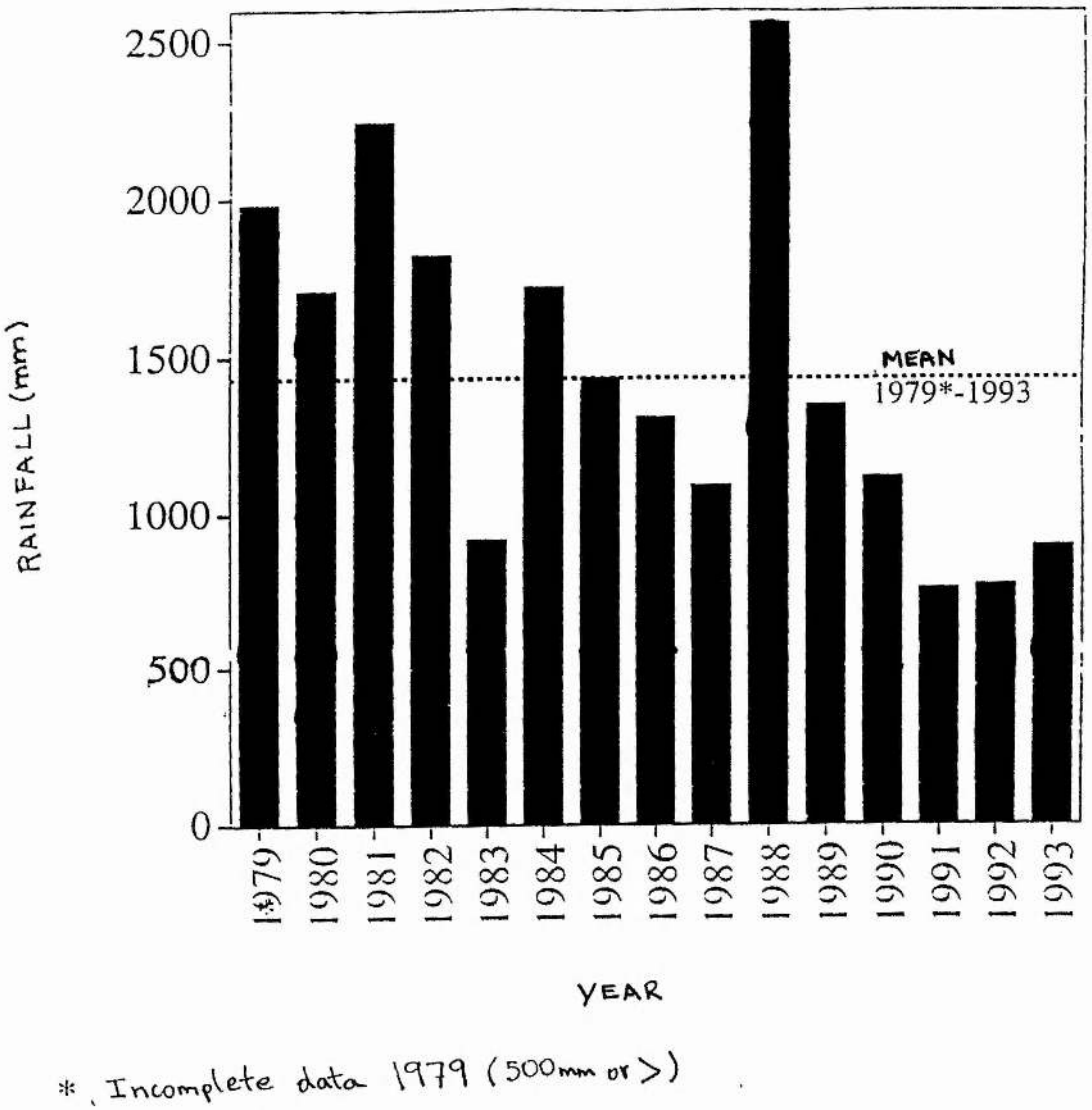


Figure 2.4. Rainfall at SRNP during the period 1979-1993 (D.H. Janzen, personal communication).

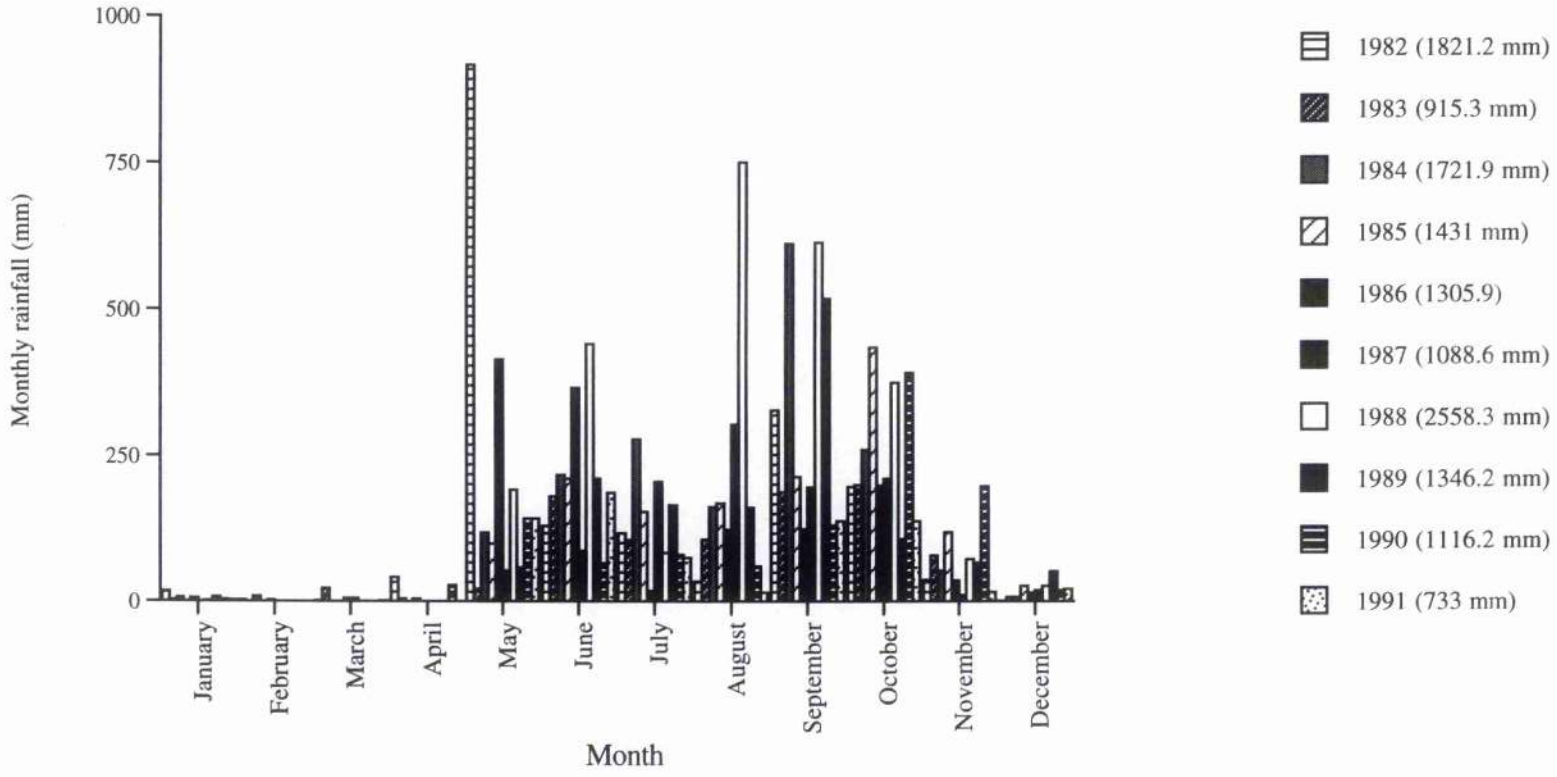


Figure 2.5. Monthly rainfall at SRNP from 1982-1991 (D.H. Janzen pers. com.)

b) Mangrove swamps
c) Dry forest marine intertidal
d) Islands and fresh and brackish water seasonal marshes
e) Post-mangrove *Prosopis* swamp
f) Alluvial semi-deciduous bottomland forest: behind the coastal beaches there were once tens to hundreds of hectares of flatland forest on rich and moist alluvial soil, containing several species of evergreen trees (i.e. *Brosimum alicastrum*, *Manilkara zapota* and *Terminalia oblonga*). In Santa Rosa these forests were severely but patchily cut; however, within SRNP 14 years of protection has allowed them to replace all fields and pasture with 3-20 m tall secondary woody succession that contains the original animals (i.e. primates in Playa Naranjo) and plant species.
g) Strongly deciduous hillside forest: the sides of the Santa Rosa plateau present a complex deciduous forest ranging from 2 m tall and totally deciduous in the dry season to 30 m tall with as many as half of the trees evergreen. A salient feature of this forest is that after it is cut, the woody regeneration that appears in its place is much more deciduous than was the original.
h) Evergreen canyon forest: the small canyons of the SR plateau bear a nearly evergreen forest that is 30-plus m in height and dominated by guapinol (*Hymenea*), tempisque (*Mastichodendron*), ojoche (*Brosimum*), and nispero trees (*Manilkara*). As with the deciduous forest mentioned above, when this evergreen forest is cleared it first regenerates as strongly deciduous secondary successional forest. These evergreen forests are extremely important local moist refugia for animals of the deciduous forest during the dry season (e.g. during the dry season spider monkeys spend larger proportions of their time in the evergreen forest patches of the study area than in the deciduous ones; see location of these patches in figure 2.6., vegetation map).
i) Evergreen oak forest
j) Pastures

Nowadays, the vegetation of the park is recovering and forms a complex mosaic of abandoned pastures, secondary growth savannahs, deciduous and semi-evergreen forest (see figure 2.6.). I have marked in the map with a black circle the study area in which the spider monkey's population ranged. It contains the different habitats used by the monkeys: evergreen riparian forest, deciduous forest, mixed forest and early secondary forest. Plate 2 shows a view of the study area (Bosque San Emilio) in the dry season.

Some of the tree species in these habitats attain 30 m in height, but the canopy is generally about 20 m tall. Common deciduous tree species include *Spondias mombin*, *Luehea candida*, *Luehea speciosa*, *Guazuma ulmifolia*, *Bursera simaruba*, *Casearia arguta*, *Chomelia espinosa*, *Pithecellobium saman*, *Tabebuia ochracea* and *Chlorophora tinctoria*.

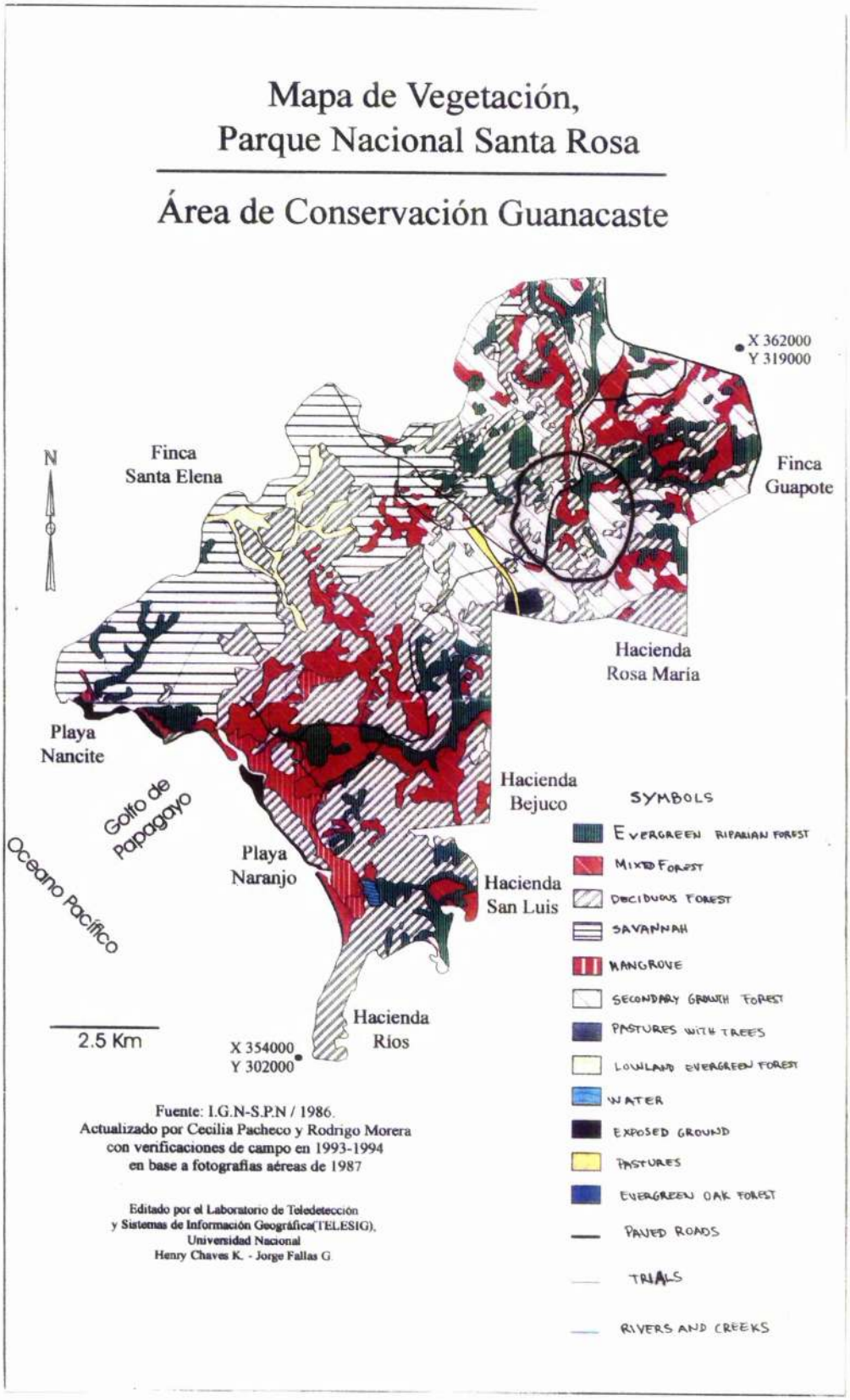


Figure 2.6. Map of the vegetation of SRNP. Location of study area marked with a black circle.

Plate 2. View of the study area (Bosque San Emilio) in the dry season.

Some examples of abundant evergreen trees include *Hymenaea courbaril*, *Mastichodendron capiri*, *Ficus*, *Manilkara zapota* and *Ardisia revoluta*. Several seed-eating and frugivorous mammals function as seed dispersers for some of these species. For example, spider monkeys and white-faced monkeys are seed dispersers of *Bursera simaruba*, eating the whole fruit, whereas other seed dispersers (squirrels, peccaries) strip off the outer covering and drop the hard seed (Janzen 1986).

2.1.4. Fauna

In SRNP there are approximately 115 species of mammals, among which one may find white-tailed deer (*Odocoileus virginianus*), coatis (*Nasua narica*), racoons (*Procyon lotor*), peccaries (*Tayassu tajacu*), Baird's tapirs (*Tapirus bairdii*), anteaters (*Tamandua mexicana*), three-toed sloths (*Bradypus variegatus*), jaguars (*Felis onca*), ocelots (*Felis pardalis*), tayras (*Eira barbara*) and three species of monkeys, howler monkeys (*Alouatta palliata*), white-faced monkeys (*Cebus capuchinus*) and spider monkeys (*Ateles geoffroyi*); around 275 species of resident birds and 16 migrant ones. There are more than 150 species of reptiles and amphibians. A few characteristic reptiles are the rattle snake (*Crotalus durissus*), the boa constrictor (*Boa constrictor*) and the Olive Ridley turtle (*Lepidochelys olivacea*). Aproximately 30,000 species of insects can be found of which 3140 are moths and butterflies, and 750 species of plants.

Although some of this fauna is representative of that of dry forest throughout Pacific Mesoamerica, some animals such as sloths, tapirs, spider monkeys or parrots are typical 'rainforest animals' that occur in SRNP but at lower densities or as seasonal members of certain habitats. Moreover, many of the less mobile animal species in Guanacaste's Conservation Area dry forest belong to a population that is morphologically distinct from the same species on the wet side of Costa Rica. For example, in SRNP individual birds, moths and monkeys are smaller and lighter in colour than their rainforest conspecifics. It is not known how much of this difference is genetic and how much is an ecological expression of the shorter rainy season, longer dry season, greater isolation and greater temperatures (Janzen 1983). To a smaller scale, even individual spider monkeys of the population studied in the dry forest of SRNP were of a smaller size and lighter in colour than their conspecifics ranging in the nearby more moist areas (evergreen forest) up in the volcanoes (i.e. Rincón de la Vieja or Cacao volcanoes).

2.2. GENERAL METHODS

2.2.1. Habituation and identification of the monkeys

Although the community of spider monkeys on which I focused was habituated by Chapman who studied it over a six-year period (1983-1989), the monkeys had not been continuously observed or followed since the year 1989. Chapman did not find habituation a difficult task with this species (Chapman pers.comm.). However, during the first months of my study some individuals showed signs of uneasiness when detected by observers and reacted with barking, scratching, branch-shaking, defecating on top of the observers in a few occasions (taking careful aim at their target) and fleeing from the site. When this occurred, my assistant and I followed them silently at a greater distance, trying not to make any sudden movement and never looking straight at them. Other individuals seemed habituated to the presence of observers and ignored us completely at these early stages of the study. There were never more than two observers. After the third month of the study most individuals of the community were habituated to us and we could follow them from a distance of up to 15-20m, without seeming to affect their behaviour. Only in two separate occasions two adult females who had never reacted to our presence before, showed signs of distress when being followed, i.e. gave *squeals* and branch-shaked to us. The reason for this change in behaviour may have been that each of them had just given birth to a new infant (2-1-94; 15-6-94) and were thus behaving more defensively. There was also a difference in reaction to observers depending on the location where the encounter took place. If the monkeys met us at places where they were used to meeting people, such as while they were ranging in the camp area, near the paved road that runs across the forest, or in one of the trails we used in the study area, they did not react but continued their normal activity. However, when they saw us in deeper parts of the forest where there were no trails and in which we were not usually seen, they generally seemed more anxious and took a longer time to resume their previous activity. Whenever we followed unhabituated spider monkeys at other sites within the Guanacaste Conservation Area, they invariably reacted with barking, and fleeing.

For the identification of the monkeys I could sometimes rely on collars or ankle bands; 14 individuals were marked by Glander et al. (1987) for radio tracking between 1985-1986, of which I only saw two marked adult females (possibly the other monkey's collars or ankle bands had worned out and fallen down). Other characteristics that proved to be useful in identifying individuals were pelage patterns, the colour of the skin or spots in the face, and the pitch of some of their vocalizations. By the seventh month of the study I could recognize an adult female and male by the pitch of their *whinny* calls. I assigned a

name to each identified monkey, related to some physical feature of its face, and used its initials for data collection and analysis. I used a pair of 8x40 Zeiss binoculars for individual identification and behavioural data collection.

2.2.2. Locating the monkeys

Locating the monkeys was a major problem at the start of the study, when I did not know well the trails of the area, and I was not aware of the monkeys' routine. This problem became worst in the dry season, when the very strong winds that characterize this season made it very difficult to see or hear the calling of such an extremely arboreal primate (spider monkeys in SRNP have been seen coming to the ground to drink from a water hole in only two occasions in the dry season; Rodrigo Morera, pers.comm.) Once I became used to the routine of the monkeys, I located the sleeping sites and fruiting trees that were being used at the time, and marked them in a map of the area. If I knew where the monkeys had slept on one night, I went to the sleeping tree the next morning, waited for their awaken, and started following them. If I knew the location of a big fruiting tree where the monkeys were eating regularly, I waited a few hours in it for their arrival. If these two strategies failed to work, my assistant and I walked separately along trails at opposite ends of the study area searching for the monkeys, trying to cover the maximum possible number of trails, and communicating every 15 minutes with a walkie-talkie. We frequently heard the monkeys calling (e.g. loud calls or barking) before we could actually see them. In these occasions we followed the direction of the sound and walked towards it. This worked out specially well if it was a stationary monkey alarm calling. Once we found a single individual, it eventually led us to other monkey subgroups.

There were times when we did not make any contact with a single spider monkey for a whole week. In two of these occasions I decided to use a different method to find the monkeys. The method of playing back a call to locate spider monkeys was already used by Klein (1972). He played back '*whoops*' (calls used to locate other members of the social group) to *A.belzebuth* in Colombia. They responded to these playbacks by giving *whoops* as well. I played back the 'long call' (*whoop*; Van Roosmalen and Klein 1988) of an identified individual recorded in the area. Long calls are frequently given by solitary animals who are trying to retrieve contact with a subgroup (they are audible at a distance of 800-1000 m). We set up the speaker in the top of a hill, in an area in which the sound could travel furthest and from which we could have the widest field of vision. While I played this long call and scanned the area around the hill, my assistant moved 500m in the opposite direction of the speaker and listened attentively to any response that monkeys nearby could give to the playback. We tried this procedure only two times (21-4-94; 6-6-94), exclusively as a method of locating the monkeys. In both trials unseen monkeys in the nearby area responded with long calls and barking; in one trial they approached the

playback site. This allowed us to see them and follow them. Only one of us followed them to their sleeping site and waited for an hour before starting to collect any data.

2.2.3. Study subjects

The genus *Ateles* is distributed over a wide area, in Central and South America. *Ateles geoffroyi* occurs from Mexico through Central America to eastern Panama (Napier 1976). There are three subspecies of spider monkey in Costa Rica, *A.g.frontatus*, *A.g.ornatus* and *A.g.panamensis*. The spider monkeys in SRNP belong to the subspecies *A.g.frontatus*. According to the IUCN Mace-Lande categories for the conservation status of New World primates, this subspecies is considered to be vulnerable, that is, facing a high risk of extinction in the wild in the medium-term future (Rylands 1995). Although spider monkeys are present in most sectors of the Guanacaste Conservation Area (Santa Rosa, Murciélago, Junquillal, Cerro el Hacha, Pitilla, Cacao and Rincón de la Vieja; see figure 2.2.), they have only been studied in Santa Rosa. Chapman et al. (1989) censused the three primate species present in Northwestern Costa Rica in some of these sectors and found that spider monkeys were able to survive in protected areas of young regenerating forest in which they have access to large areas of forest patches. The density of spider monkeys at the time in the whole of the Guanacaste Conservation Area was 4.5 individuals per square kilometre.

The study community consisted of 60 individuals of a population of 190 in the whole SRNP (the last spider monkey census in the whole park was carried out in 1992; Rodrigo Morera pers.comm.). Of these 60 individuals I could identify 15: 11 adult females, one adult male, one subadult female and two juvenile females. Table 2.1. shows some characteristics of these identified individuals. The average weight for an adult male spider monkey is 8.37 kilos, for an adult female is 6.62 kilos and for a juvenile female, 4.0 kilos (Fedigan et al. 1988). The age-sex classes used in the study were defined using van Roosmalen and Klein (1988) criteria:

- Adults: large size individuals, with fully developed genitalia. The males show darker faces than the females, who have paler skin around the eyes. The females have an external pendulous clitoris which has been hypothesized to be adapted to deposit drops of urine as scent marks of passing places or resting locations (Klein 1971)(see plate 3; adult female with visible external clitoris. Adult males might sniff these marks to find out about the sexual state of a female (see plate 4; adult male).

Table 2.1. Name, age-sex class and number of offspring of identified individuals in the study.

Name	Age/sex class *	Offspring
AM M1 (AM M1)	Adult male	-
AF Viejita (AF V)	Adult female	Infant female+juven.female
AF Tobi. Azul (AF TA)	Adult female	Juvenile female
AF Chancho (AF CH)	Adult female	Infant born 15-6-94
AF Soñolienta (AF S)	Adult female	None
AF F1 (AF F1)	Adult female	Infant female+juven.female
AF Nostril B. (AF NB)	Adult female	Infant female born (2-1-94) +juven.female
AF Diablillo (AF D)	Adutl female	None
AF Collar Rosa (AF CR)	Adult female	Infant female
AF D.Nostril B. (AF DNB)	Adult female	Juvenile female
AF DViejita (AF DV)	Adult female	Juvenile male
AF Amistosa (AF AM)	Adult female	None
AF Independ. (AF IND)	Subadult female	None
Juvenile fem.F1 (JV F1)	Juvenile female	None
Juvenile fem. NB (JV NB)	Juvenile female	None

* Following van Roosmalen and Klein (1988)

Plate 3. Adult spider monkey female with external clitoris visible.

Plate 4. Adult spider monkey male scanning.

- Subadults (50-65 months): their body size is almost equal to that of adults but subadults are less robust. They can also be distinguished from adults by their paler face colour and pigmentation. Some subadult females spend large amounts of time with their mothers. Subadult males associate with other males and range completely independently from the mother (see plate 5; subadult male foraging).
- Juveniles (12 months to 3.5 years old): individuals who usually locomote independently during group progression, but remain with their mothers the rest of the time and are still nursed.
- Infants: have a very pink mask around the eyes and mouth. They are always clinging to their mother's ventrum or riding on her back, and never locomote independently between food sources.

2.2.4. BEHAVIOURAL DATA COLLECTION

General

During data collection there was usually a local assistant working with me, Mariano, Hugo or Minor (each at different times of the study), who did not participate in the collection of behavioural data but always kept track of the monkeys, their group size, composition, and the approximate age-sex classes of callers who were out of my field of vision. They also helped me carrying out playback experiments and identifying plant species eaten by the monkeys. The amount of time we followed a certain subgroup of monkeys varied widely, depending on several aspects: the weather conditions (we lost track of the monkeys more frequently when it was windy), their speed of locomotion, whether they followed the trails or they ranged deep into areas of the forest where no trails have been cut, or their subgroup size (it was easier to follow smaller than larger subgroups because the latter tended to fission suddenly and confuse the observers). Most longer follows took place in the morning, in days when we found the monkeys still in their sleeping site and we followed a subgroup as the group was splitting up. At the beginning of the study I started recording data on check sheets while I was following the monkeys, but I realized in a few days that they moved too fast and I lost large amounts of information as I was writing it down. Therefore, I decided to describe the monkeys' behaviour onto a small dictaphone which allowed me to do two things at the same time, i.e. look at the monkeys and describe their behaviour as they were moving from one location to the other. I transcribed this information onto check sheets every night.

Plate 5. Subadult male foraging on *Guazuma ulmifolia* fruits in the dry season.

Sampling methods

Different sampling methods were employed simultaneously in observation sessions during the study since a variety of questions were being explored. The total observation times given below for each method do not include the time spent in the forest searching for the monkeys.

i). Focal behaviour sampling

During the first period of the study (first three months) I was particularly interested on habituating and identifying the monkeys, locating the density and distribution of their food resources and becoming familiar with the most commonly used calls of their repertoire. Therefore, each time a subgroup was encountered a focal behaviour sampling (Martin and Bateson 1986) with 10 minute interval point samples was used to record several aspects of their feeding and vocal behaviour. The following information was recorded at every point sample:

a. Feeding: the size of the tree measured by its DBH (diameter at breast hight), the species and part eaten by the monkeys (fruits, leaves, flowers) was noted. The location of the tree was marked in a map, together with whether or not it was a sleeping site.
b. The group size and its composition.
c. Activity. If they were not involved in feeding or calling the following general activities were scored: resting, grooming, moving, or drinking.

Vocalizations. The occurence of any type of call in the spider monkey's repertoire (see catalogue of vocalizations in appendix I) was recorded continuously, together with the context in which it occurred, the group size and its composition. All vocalizations which are specific to spider monkeys will be written in italics from now onwards. A total of 128 hours and 40 min of this type of data was recorded.

ii). Focal animal samples

From the fourth month of the study onwards I started doing focal animal samples, which consisted of a combination of continuous and point sampling (Altmann 1974). Instantaneous (point) samples were taken at 10 minute intervals, recording:

a. Location of the focal animal in a map of the study area.
b. Activity of the focal animal (forage, move, drink, eat , rest, groom)(see description of categories in ethogram, in appendix II).

c. Subgroup size and composition.

d. Vigilance state (0-4)(see definitions in appendix II).

During each focal sample the following data were recorded every time they occurred (see description of behaviour categories used in appendix I):

a. Vocalizations:

- type of call
- time of occurrence
- identity of caller (if the caller could not be identified I registered its age-sex class, and the size and the composition of the subgroup it was in)
- context surrounding the call
- response of receivers of the call
- identified individuals within hearing distance.

b. Aggressive behaviours.

c. Submissive behaviours.

d. Affinitive or contact-promoting behaviours.

e. Sexual-olfactory.

f. Other behaviours.

Not all of these behaviours were analyzed in this thesis because the frequency of occurrence of some was very low and others were never observed since they might have taken place under the canopy, out of sight.

Sometimes I lost the focal animal because it was travelling faster than I was able to follow through dense vegetation. Whenever I lost sight completely of a focal animal, I stopped collecting data ('time out' was scored). If after a 15min search I could not find it again, I started a new sample with another individual or searched for another subgroup.

Focal animal samples were conducted on 12 of the identified individuals: 11 adult females and one adult male. A total of 55 focal samples were collected, with an average of five focal samples per individual (see table 2.2.). The average duration of focal samples was three hours (range 1-5). A total of 113 hours of focal data was recorded.

iii). Data collection on all occurrences of a type of call: the *whinny*

This type of data was recorded from the second up to the last month of the study. A focal behaviour sampling on emission of *whinnies* was used in a continuous recording fashion. Each time a *whinny* occurred I recorded: the identity of the caller or its sex/age class (if the identity was unknown), the context in which the *whinny* was emitted, the subgroup size, the vigilance state of the caller, and the responses of the receivers. If the

Table 2.2. Number of focal samples per identified individual and total observation time (not including observation time during vocal recordings).

Individual	#Focals	Total observat.time
AM M1	13	27h
AF V	5	6h50m
AF TA	3	6h20m
AF CH	2	3h
AF S	1	1h50m
AF F1	7	17h
AF NB	9	19h
AF D	2	4h
AF CR	4	4h50m
AF DNB	4	5h
AF DV	3	13h
AF IND	2	3h40m

call was given while feeding, the tree species, the resource used, the DBH of the tree, and its location was noted. A response was defined as any behaviour or vocalization occurring within 10 seconds after the emission of a *whinny*. Using this sampling technique 47 hours of observations on *whinny* emission were collected.

Halfway along the study (April 1994), while I was still on the field, I conducted a preliminary analysis of the first five months' data on the frequency with which *whinnies* were given in different contexts and the most common responses to them.

iv). *AD LIBITUM* sampling: tape recording of vocalizations

Ad libitum sampling refers to non-systematic techniques for recording behaviours in which no rules are followed in the choice of behaviours, individuals, or the times of sampling sessions (Altmann 1974). This was the method used for collecting data on vocalizations of spider monkeys, particularly their *whinny* calls and alarm calls.

All recordings were from both identified and unidentified spider monkeys of the community of Santa Rosa. The total vocal recording time was 58 hours. In the first months of the study I used the program Sound Edit Pro to inspect visually spectrograms of the vocalizations recorded in order to find any common pattern and verify the quality of the recordings.

Vocal recordings were also conducted in other sectors of the Guanacaste Conservation Area (see locations marked in figure 2.2.). Sectors with different forest types were chosen in order to investigate if the acoustic structure of the *whinny* varied depending on the habitat the monkeys lived in. Unfortunately, the call sample recorded was not big enough for analysis to be conducted, and the recordings were not of high quality due to the large recording distance that we had to keep between us and the unhabituated monkeys, to avoid scaring them away. The total vocal recording time at these sites was 12 hours and 45 minutes.

Ad libitum records were also kept on any instance of predator, intercommunity, and interspecific encounters.

2.3. DEFINITION OF AMBIGUOUS TERMS: community, subgroup, group

In this study the terms community, subgroup and group will be used according to the following definitions (following van Roosmalen and Klein 1988; Chapman 1990):

Community: a number of animals that use the same home range area, interacting usually peacefully with one another. Communities are separated from one another by agonistic interactions conducted mainly by males. A specific feature of a community of spider monkeys is that it is rare to find all of its members at the same place. Most spider monkey's studies have used the term 'group' to refer to a community but in this study I will use it with a different meaning.

Group: large associations of spider monkeys that usually take place at night in sleeping sites, or during the day in big fruiting trees which hold a large fruit crop. It does not have the unstable and short term character of the spider monkey's subgroup, but is instead more permanent.

Subgroup: any number of individuals, less than the total community or the group, that associate together, taking part in coordinated activities, and maintaining relatively close spatial contact (Chapman 1989). Subgroups are extremely temporary, and may change their composition several times per day or even hour.

Chapter 3
Spider monkeys. Feeding and ranging behaviour

In this chapter I summarize some important aspects of spider monkeys' feeding and ranging behaviour, which will serve as an introduction and give relevant information for the subsequent experimental chapters. Special emphasis will be given to issues that can be generalized across different *Ateles'* species. Since this population has been studied for a considerable amount of time, I will briefly describe some of the results found in previous research, connecting them when possible to my own findings on the same community. Although my study did not focus specifically on feeding ecology or ranging behaviour, I did collect some systematic information on these issues.

3.1. FEEDING

Feeding behaviour of *Ateles*

All *Ateles* species are predominantly frugivorous and feed mainly on the mature parts of a wide variety of fruits. Other components of their diet are: young leaves, flowers, bark, floral buds, and insects (e.g. caterpillars). Spider monkeys frequently ingest large quantities of fruits within brief periods of time (e.g. 100 fruits of 20 mm in diameter in a seven-minute period; Klein and Klein 1977). When they eat fruits, they generally swallow seeds intact without mastication (seed dispersal), but sometimes they drop the seeds after the softer edible parts have been removed (seed dropping), or with certain families of seeds, they eat them in an unripe stage and destroy them in the digestion process (seed predation)(van Roosmalen and Klein 1988). Few cases of manipulation have been observed in spider monkeys feeding on fruit. Spider monkeys appear to select for variety, trying to maximize the number of fruit varieties eaten every day. In any given month there seem to be three or four food items which are the most important in terms of the amount of feeding time spent eating them. The duration of feeding visits to these 'primary' food sources may be quite long, but never exceeding two hours (*A.p.paniscus*, Van Roosmalen 1980; *A.b.belzebuth*, Klein and Klein 1977). Because most species on their diet have seasonal periods of fruiting and flowering, spider monkeys have adapted their feeding strategy to this seasonality (e.g. *A.p.paniscus*' energy budget is positively correlated with the total number of food species available each month. Van Roosmalen 1980). In relation to the strategies adopted, an important result found by van Roosmalen in Suriname was that in *A.p.paniscus* the daily itineraries and the activity patterns of a subgroup were

determined by a leading (usually most aged) female. These females seemed to know best the location of highest quality food resources in the home range. Thus, they regularly checked the maturity stage of resources and chose a foraging route for a particular day in a predetermined fashion, followed by the rest of the subgroup. Therefore, the social structure of spider monkeys seems highly efficient for exploiting the available mature fruit sources, specially since other group members can learn about these food sources through conspecific cueing, i.e. through vocalizations such as the *whinny*, which seems directly associated with food source characteristics, such as food quantity (see next chapter, Chapman and Lefebvre 1990).

Feeding of *Ateles geoffroyi* in Santa Rosa National Park

Chapman (1987; 1988b) studied the three species of primates living in Santa Rosa National Park (spider monkeys, howling monkeys and white-faced monkeys). He found that the diets of all three species varied considerably on a monthly and annual basis (both in the types of food consumed and in the plant species exploited). For example, the diet of spider monkeys varied from being composed of exclusively fruit in a certain month to consisting of primarily leaves in another. He concluded that competition between these species is unlikely to play an important role in determining their diet (Chapman 1987). Although Santa Rosa National Park is characterized by two very extreme wet/dry seasons in which food availability differs markedly, he did not find any clear differences in spider monkeys' diet that could be related to the shift in season. A possible explanation he suggested was that many plants have coevolved with the animals that disperse their seeds; thus, monkeys are more likely to respond to the phenological cycles of specific food plants than to season (Chapman 1988b). Spider monkeys spent the greatest proportion of their feeding time eating fruits that tend to be rare and located in patches that are far apart from each other (Chapman 1988a). Spider monkeys' diet (total feeding time spent eating different types of food) during a four year period (1983-1986) was the following:

- fruits: 77.7%
- flowers: 9.8%
- leaves: mature 1.2%, young 7.3%, buds 2.6%
- insects 1.3% (insect availability was greater in the wet season)

The **five most used plant species** by spider monkeys were:

- *Ficus* sp. (fruit)
- *Muntingia calabura* (fruit)
- *Mastichodendron capiri* (fruit)

- *Dipterodendron costaricensus* (fruit)
- *Pithecellobium saman* (flowers)

Monkeys spent more than 50% of their feeding efforts eating only three foods (*Ficus* sp., *Muntingia calabura*, *Mastichodendron capiri*). They were selective in their choice of food items, relying often on tree species that occurred at low densities. Individual spider monkeys often centred their feeding activity around one large food tree or repeatedly fed in several spatially separated trees, often moving between feeding sites in a set pattern during the day.

Although my study of the same community of spider monkeys as the one studied by Chapman was not focused particularly on their feeding ecology, I did collect some general data about feeding (see chapter 2, Methods, behavioural data collection). This consisted of:

- species of trees the monkeys fed on
- food type eaten
- DBH of trees
- subgroup size of feeding parties.

Some of the tree species eaten by the monkeys in the year 1994 can be seen in table 3.1. with the different types of food eaten. For some species, they only ate fruits (*Spondias mombin*), for others they only ate flowers (*Pithecellobium saman*), whereas for species such as *Bursera simaruba* they fed on all three types, fruits, flowers and young leaves (see plate 6, adult female eating fruits). *Ficus* bear mature figs only over extremely brief periods, ranging from four to ten days. *Ficus* trees were very often visited by spider monkeys in Santa Rosa National Park to examine the ripeness of their fruits. They ate in different *Ficus* trees during all months of the wet season. When they fed on *Enterolobium cyclocarpum* they only ate butterfly larvae during a whole week in May, when these trees were full of this larvae. The average size of feeding parties was three monkeys (N=115). The average DBH of the trees in which they were observed eating was 68.61cm (N=73 trees measured).

Table 3.1. List of tree species, and types of food eaten by spider monkeys in different months of the year 1994 at Santa Rosa National Park

Tree species	Type of food eaten	Month of the year
Anona reticulata	Fruits	January
Bombacopsis quinatum	Flowers and young leaves	January-May October-November
Brosimum alicastrum	Fruits	June
Bursera simaruba	Fruits, flowers and young leaves	March, April, September
Cecropia peltata	Fruits and sprouts	March, August, September
Clorophora tinctoria	Fruits	July, August
Dipterodendrum costaricensis	Fruits	April
Dyphysa robinioides	Flowers	April, November
Enterolobium cyclocarpum	Larvae	May
Ficus	Fruits and flowers	March, May-November
Genipa americana	Fruits	May
Guazuma ulmifolia	Fruits	March, April, November
Karwiskia calderoni	Fruits	January-March
Luehea candida	Flowers	November
Luehea speciosa	Flowers	January, June, December
Manilkara zapota	Fruits and flowers	January, May
Masticodendron capiri	Fruits	February, March, June
Pithecellobium saman	Flowers	March, April
Spondias mombim	Fruits	June-September
Styrax argentea	Leaves	April
Tabebuia ochracea	Flowers	May

Plate 6. Adult female eating fruits of *Bursera simaruba* ('indio desnudo').

Water Resources

Chapman (1988b) observed that during the early dry season water in the study area was available from three sources, arboreal water holes, standing water that remained in creek beds, and water contained in the monkeys' food resources. However, both the arboreal water holes and the standing water dried up before the end of the dry season (the only water left was in their foods). During his study he saw spider monkeys coming to the ground to drink from standing water holes. Although I never observed this behaviour, I did see in a few occasions spider monkeys using their hand as a sort of scoop to pick up water from holes in trees.

3.2. RANGING

Two different methods have been used in the same study to estimate home range size of the Santa Rosa spider monkey population. The average home range size of the community estimated from observational data during Chapman's study was 43.7ha (range 24.5ha to 63.4ha)(Chapman 1988b). However, the average home range size, as calculated from radio-telemetry data was 62.4ha, with considerable variation between individuals, i.e. 37.4ha for an adult female with infant; 97.9ha for the largest adult male. This sexual difference in home range supports the hypothesis (Fedigan and Baxter 1984) that male spider monkeys have adapted to female dispersion by occupying a large home range that overlaps the ranges of several females (Chapman et al. 1988). Chapman (1988b) did not find a clear difference in range use that could be related to the shift in season (dry/wet season), rather range use patterns were likely situation-dependent, i.e. in certain occasions a single fruiting tree (*Ficus sp.*) influenced the daily itineraries of the monkeys during the whole period in which the tree bore fruits.

Spider monkeys travelled in relatively small subgroups (mean=4.94 individuals) which changed size and composition frequently (Chapman 1990a). When examining the ecological determinants of subgroup size in this community, Chapman (1990b) found that when food resources were relatively scarce and located in patches that were far apart (e.g. January-April), spider monkeys were found in small subgroups. By contrast, when food was abundant or uniformly distributed (e.g. September-October), spider monkeys congregated in large subgroups. Males ranged often in all-male subgroups, which ranged further and travelled faster than subgroups with females and young. The adult females with either infants or small inmatures tended to be seen frequently in a central area and thus have a more clumped pattern of distribution, whereas females without immatures were more evenly dispersed in the use of their range. When a female was accompanied by an offspring she tended to concentrate her activity in a small area, but if she was on her

own she tended to range more widely. Moreover, females with dependent offspring were more solitary and ranged in smaller subgroups than males or females that did not have infants. By being in small subgroups these females may decrease feeding competition (Chapman 1990a).

Since much of the spider monkeys' home range in Santa Rosa is surrounded by grasslands or young regenerating forest, contact with neighbouring communities could only take place along the community's northern boundary. Although no territorial encounters have been observed at Santa Rosa, on 31 occasions members of other communities were seen to enter the home range of the Santa Rosa community (Chapman 1990). The boundary of the community's home range is used frequently by males and females without infants, but rarely by females with infants.

Evidence of these typical ranging patterns can be seen in figure 3.1. which shows a map of my study area with examples of the daily itineraries of three focal subgroups. A subgroup of males had the longest day range and ranged nearer the territory boundaries, whereas an adult female with her infant and juvenile daughter stayed in a more central area of the territory. An adult female without dependent offspring was seen one day (8-5-94) ranging near one of the boundaries of the territory, an area rarely frequented by females with offspring.

During my study I recorded general data on subgroup size during focal animal sampling (see chapter 2, Methods) and drew the daily itineraries of focal subjects in a map of the area. In figure 3.2. it can be seen how the average subgroup size of the monkeys varied in different months of the year 1994. The months in which subgroups were largest (more than four monkeys) were February, June and July. Although the data sample is small (N=105 subgroups observed) to compare it with Chapman's (1990a) results commented above, I wanted to mention that in two of those months when subgroups were largest, i.e. June and July, the monkeys were feeding mainly on the fruits of *Ficus sp, Mastichodendron capiri* and *Spondias mombin*, trees all of which produce large amounts of fruit that can sustain large numbers of monkeys feeding on them at the same time. However, in the month of February the monkeys were feeding mainly on the flowers of *Bombacopsis quinatum*, which is represented in the study area by individual trees of large sizes (e.g. one individual had a DBH=3.05m) that harvest large quantities of flowers dispersed in its branches, able to feed a large number of scattered monkeys. While spider monkeys are travelling through their home range from one feeding or resting site to the other it is common to hear them calling, as if they were locating each other by means of reciprocal calls.

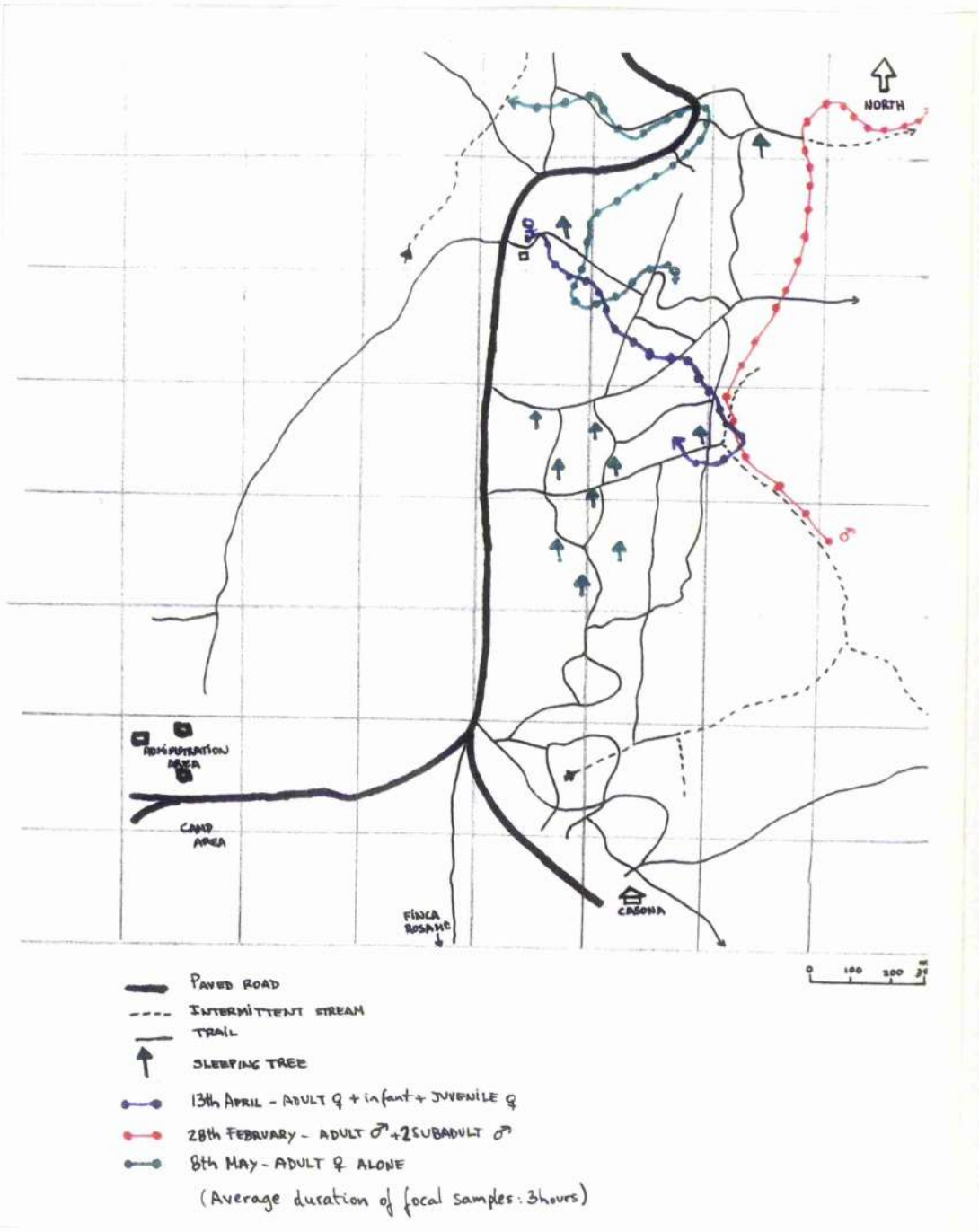


Figure 3.1. Map of the study area with daily itineraries of three different subgroups of spider monkeys and location of sleeping sites during the year 1994.

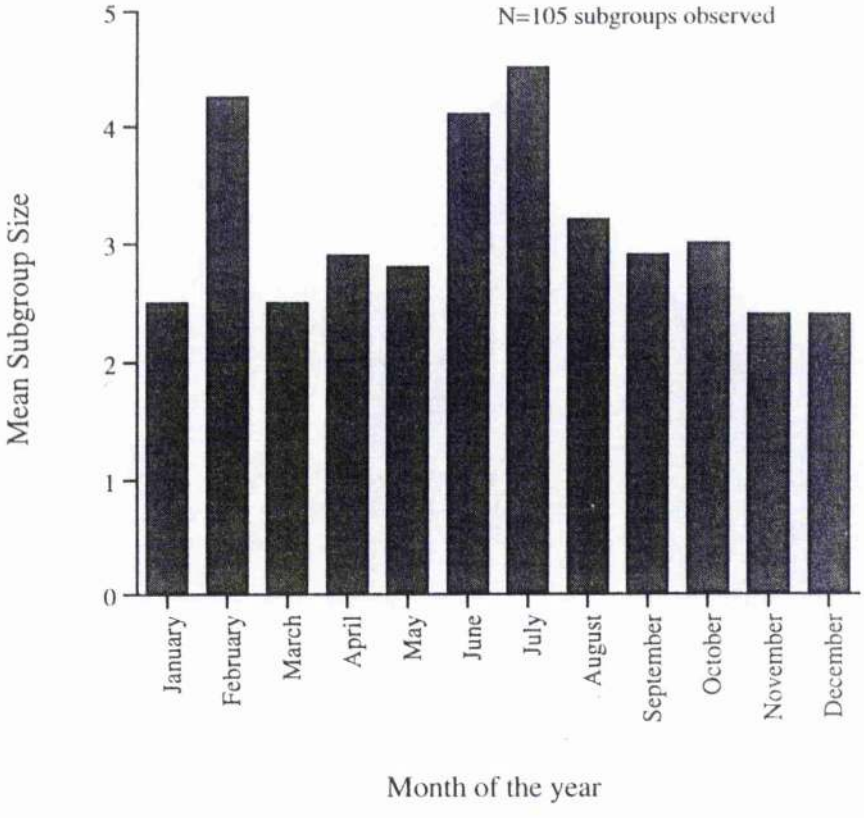


Figure 3.2. Average size of spider monkeys' subgroups observed in each month of the year 1994

The route taken by some adult females appeared to be preplanned and highly economic (rarely doubling back), as if they knew the exact location of the important food sources. Several sleeping sites used by spider monkeys during the year 1994 have also been marked in the map in figure 3.1. During the year of 1994 spider monkeys used 14 different sleeping sites, some of which were repeatedly used but never on two consecutive nights. These trees were of large size (mean= 92.8cm DBH). Some of the most commonly used species were: *Enterolobium cyclocarpum, Mastichodendron capiri*, and *Hymenaea courbaril.* When spider monkeys entered a sleeping site in which other subgroup were already present they often emitted loud 'greeting' vocalizations, *whinnies,* that were responded by the monkeys occupying the tree with loud *whinnies* as well. Sometimes there was a chorus of *whinnies* as a subgroup was entering a sleeping site for the first time; this calling may function to attract nearby parties to form a larger unit for the night.

When a subgroup of spider monkeys entered a fruiting tree in which a group of howler monkeys were already eating or resting, the two species of primates either ignored each other and ate peacefully next to each other (n=6), or the howler monkeys avoided spider monkeys by moving away from the tree (n=4). However, when spider monkeys encountered a subgroup of white-faced monkeys in a fruiting tree, the outcome of the encounter was more variable. It seemed to depend on the size of both species' subgroups. If the white-faced monkey's subgroup was largest, the two species ate in the same tree but spider monkeys tried to chase white-faced monkey from the branches with more fruit (n=4). However, if spider monkeys outnumbered the white-faced, the latter moved away from the tree (n=3).

3.3. SUMMARY

Spider monkeys were very selective in the choice of food items they fed on. In Santa Rosa National Park, they were, as most *Ateles* species, mainly frugivorous, although a second important component of their diet was flowers. Spider monkeys very often called when they entered a fruiting tree or while they were feeding on it.

There were no apparent differences in the ranging behaviour of spider monkeys in the dry versus wet seasons, but their ranging patterns seem to be situation-dependent. In my study the largest subgroups were observed in months during which there were fruiting trees producing large crops of fruits or flowers (February, June, July). Calling frequently occured when travelling from one place to the other or entering sleeping sites.

Chapter 4
The use of the *whinny*: a food call or a locational call?

INTRODUCTION

The *whinny* is often the most frequently heard vocalization from spider monkeys. In one of the earliest descriptions of the *whinny*, Carpenter (1935) described this call as occurring when subgroups or individuals become separated, serving to coordinate the movements of subgroups within a 'clan' (community). Later, Eisenberg and Kuehn (1966) described it as a feeding call, functioning in the maintenance of spatial awareness or assembly, but not promoting physical contact. Eisenberg's (1976) detailed study of captive and free-ranging spider monkeys' communication mechanisms basically concluded the same as in his study of 1966, but incorporated the suggestion that *whinnies* may be position indicators that serve to indicate availability of food and appear to reflect a non-hostile mood. He claimed that *whinnies* do not carry far and the most common actions by receivers when hearing them are to give a *whinny* back, and to approach and join the caller. Klein (1972) emphasized that the *whinny* is regularly heard during subgroup mergers. He observed that *whinnies* were initiated when at least one of the members of two different subgroups were first able to see another individual or the characteristic pattern of branch movements made by a spider monkey approaching. He described the vocalization as frequently reciprocal and noted its use in various contexts:

- when an adult spider monkey first entered a tree bearing ripe fruit
- in response to loud vocalizations (*whoops*, *wails* or *squeacks* made by other spider monkeys in the distance)
- in response to a sudden sighting of the observers
- in response to a direct stare of either a conspecific or observer
- in response to a *whinny* of another individual
- by females as they retrieved their infants

It is important for later discussion to remember Klein's (1972) conclusion: '*whinnies* appear to be a vocal reaction to mildly arousing and perhaps ambiguous social and environmental stimuli'. This idea is consistent with a 'motivational' perspective held by some ethologists, according to whom animal signals lack the capacity to function in a symbolic manner but instead differences in call meaning are derived from changes in contextual parameters (see Introduction, Marler et al. 1992).

Most of the studies reviewed above seem to agree in describing the *whinny* either as a feeding or a locational call. However, a common aspect in all of them is that the *whinny* is emitted under very varied social circumstances (e.g. Klein's 1972 list of contexts). This raises the possibility that there may be more than one sort of *whinny*. This is the case with the 'coo' call of Japanese macaques (*Macaca fuscata*)(Green 1975), which is used in a variety of social situations, the 'coos' of stumptail macaques (*Macaca aractoides*) (Lillehei and Snowdon 1978), and the 'grunt' in vervet monkeys (*Cercopithecus aethiops*)(Cheney and Seyfarth 1982). *Whinnies* of spider monkeys may therefore have different meanings depending upon the context in which they are given.

Chapman and Lefebvre (1990), in a study investigating whether *whinnies* function to manipulate the size of feeding groups, found that spider monkeys in Santa Rosa National Park called more frequently when fruiting trees were large, when food was abundant and when subgroups contained high-ranking individuals. Therefore, they concluded that spider monkeys can conditionally broadcast information to manipulate their subgroup size in a way that minimizes feeding competition. They found no sexual differences in the frequency of *whinnies*. However, in their study they did not analyze *whinnies* on an individual basis but described them as the 'number of calls per subgroup', and only took into account *whinnies* given in a foraging context.

During my study at Santa Rosa National Park the *whinny* was the most common vocalization I heard, and by listening to *whinnies* given in different contexts or by looking at preliminary sonograms in the field I could not discriminate between them.

In this chapter I investigate the functional characteristics of the *whinny*, focusing on the following questions:

(a) Do responses to*whinnies* given in different contexts differ?

(b) Are there two functionally distinct *whinnies*, a locational and a feeding one?

(c) What information do *whinnies* convey?

I first describe observational data on the contexts in which the *whinny* is used, and the most frequent responses to it. Moreover, using my own data I will relate several aspects of the monkeys' feeding behaviour to their use of vocalizations (e.g. in what species of trees do spider monkeys give more *whinnies* ?)

Then, to test hypotheses about putative call function, I present playback experiments in which tape-recorded *whinnies* given in two different contexts (feeding versus locational) are played to the monkeys in the absence of the stimulus which originally elicited the calls (food, a subgroup encounter, or a call from a conspecific). I discuss the results of these experiments in the light of the possibility that *whinnies* are referential signals, as other primate calls have proved to be.

4.1. Observational data on *whinny* production

4.1.1. METHODS

Study area and subjects

Spider monkeys in Santa Rosa National Park were observed from November 1993 to November 1994. Observations were collected during both dry and wet seasons. The home range of the community studied was 62.4 hectares of dry deciduous forest with patches of semi-evergreen forest (see description of study site, chapter 2). The community included 60 individuals of a population of 190, according to the last census carried out in the whole park in 1992 (Rodrigo Morera, pers.com.). An exact description of the composition of this community is not possible because of the fission-fusion type of social organization exhibited by spider monkeys. An estimation of its size and composition was last conducted by Chapman (1988b) who estimated 42 individuals: 4 adult males, 17 adult females, 2 large immature males, 4 large immature females, 7 small immatures, and 8 infants.

Behavioural sampling

Behavioural data were collected in three different ways (described following Martin and Bateson 1986)(see also chapter 2).

a) A **focal behaviour sampling** with a 10 minute interval sample was used to record the following behaviours: feeding, moving, resting, and occurences of any type of vocalization, as well as data on location, subgroup size and composition. Approximately 128 hours of this type of observations were collected.

b) A **focal behaviour sampling** on emission of *whinnies* was used in a continuous recording fashion to collect data on the contexts in which the *whinny* was produced (see description of contexts below), the subgroup size, the caller, the vigilance state of the caller, the responses of the receivers, and the location. A response was defined as any behaviour or vocalization occurring within 10 seconds after the emission of a *whinny*. The responses scored were: approach the caller, move away, look towards the caller and call back (giving a *whinny* or other type of call, i.e. *squeal*). For the analyses of occurrence of *whinnies* during feeding bouts, I concentrated on the frequency with which *whinnies* were given in different tree species.

c) **Focal animal sampling** with 10 minute interval samples were conducted on 12 identified individuals: 11 adult females, and one adult male (see description of behaviour categories in appendix II). The average duration of focal samples was three hours (1-5). All day follows or longer focal samples were not possible to carry out because the composition of subgroups changed constantly and it often happened that I lost track of a focal monkey because it was moving at very high speed through the canopy. The decision of which focal individual to choose was based on opportunistic encounters. However, some individuals were discarded as focal subjects towards the end of the study because I already had a large number of focal samples on them. The fact that contact with females was far more frequent than with males explains why I only collected focal data on a single adult male.

I recorded all data on a dictaphone and then transcribed it onto datasheets the same day.

The definitions of the contexts in which *whinnies* were given are presented below:

* FEEDING: an individual is masticating or ingesting a food item, or foraging for it.
* RESTING: an individual is sitting or laying in a resting position, not involved in any activity and non vigilant.
* LOCATIONAL 1: an individual is entering a tree for the first time (a fruiting or sleeping tree).
* LOCATIONAL 2: an individual is joining a new subgroup.
* LOCATIONAL 3: an individual has lost sight of the members of the subgroup with whom it was travelling.
* OBSERVER/PREDATOR: an individual sees the observer for the first time that day or hears a sudden noise coming from another monkey species (e.g. howler monkey howling) or an alarmed terrestrial mammal running away (e.g. deer).

Statistical analysis

All three types of data described were considered for analyses. *Whinnies* are calls which may occur in rapid succession over short periods. For example, on one occasion a bout of 24 *whinnies* given by the same adult female took place in a 10 minutes period (vocal recordings on date 22-2-94). In order to avoid having repeated measures of the same subject, violating the independence criteria (Martin and Bateson 1986), a *whinny* was considered as a single data point when it ocurred at least five minutes after the previous *whinny* (this decision was based on the interval patterns between *whinnies* analysed in the vocal recordings; see next chapter). For statistical analysis of the

responses provoked by *whinnies* given in different contexts I used the chi-square test. Because multiple tests were performed on the same data the Bonferroni correction (Bakeman and Gottman 1986) was used to avoid the rejection of true null hypotheses (type I error). Bonferroni's correction adjusts the alpha level by dividing it by the number of tests performed. Thus, a level of significance equal or lower than 0.01 was used.

4.1.2. RESULTS

I will first describe the results of the occurrence of *whinnies* during feeding bouts. The relationship between the DBH of a tree (an estimator of fruit abundance) and the frequency of *whinnies* in a particular tree could not be investigated because of the uneven and scarce amount of observational time in different size trees. Spider monkeys gave the highest number of *whinnies* while eating in *Bombacopsis quinatum,* and *Genipa americana* (see figure 4.1.; weighted data). Common features of these tree species is that some individuals produce a larger crop of fruits or flowers than others, and in some species there are many individual trees spread out in the monkey's home range (e.g.*Luehea speciosa*, *Spondias mombin* or *Manilkara zapota*). Spider monkeys usually foraged in several individual trees of each species and seemed to give more calls when the crop was largest in a particular tree. The highest number of point samples in which *whinnies* were given occurred while eating fruits (see figure 4.2.)

A total of 993 *whinny* occurrences were analyzed. The total number of responses to the *whinnies* given in the six different contexts are presented in table 4.1. The responses were recorded from 12 identified adult females, one identified adult male, 3 subadult females, 3 subadult males, 5 juvenile females and one juvenile male. There were no statistical differences in the pattern of responses given to *whinnies* in the 3 locational contexts defined (chi-square=9.072; df=4; p=0.062). Therefore, I decided to lump for further analysis these three categories into a single locational context. The *whinnies* given in the observer /predator context did not elicit any reaction. They were not included in the analysis because the chi-square test is not valid if any cell has zero values. A chi-square on a 3x3 contigency table (see table 4.2.) showed significant differences between the responses given to *whinnies* in each of the 3 remaining contexts (chi-square=228.24; df=4; $p<0.001$). However, a significant chi-square only tells one that somewhere in the table the observed frequencies are not simply chance deviations from the expected frequencies. In order to find where the differences in the contingency table were I used (following Siegel and Castellan 1988) the method of partitioning the contingency table into subtables and analyzing each of them (see table 4.3.).

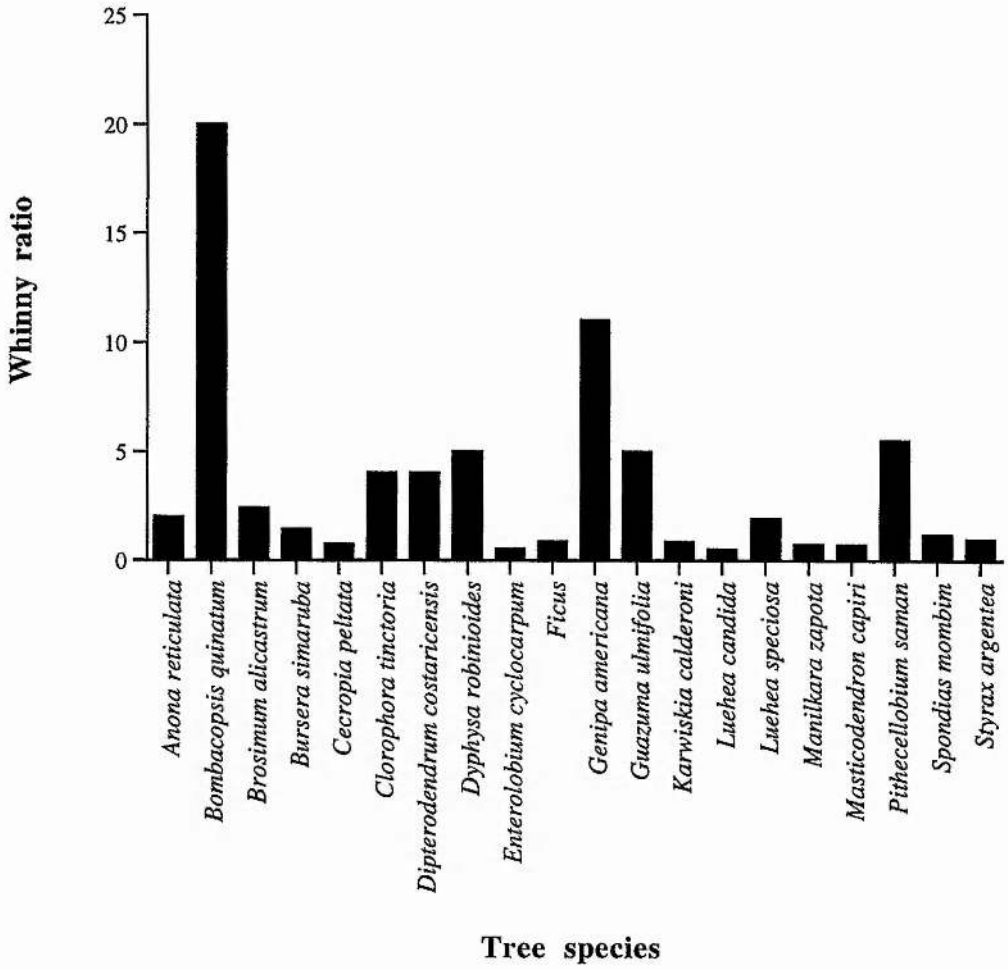


Figure 4.1. *Whinny* ratio while eating in different tree species (#whinnies/#point samples in which monkeys were observed eating in a tree)

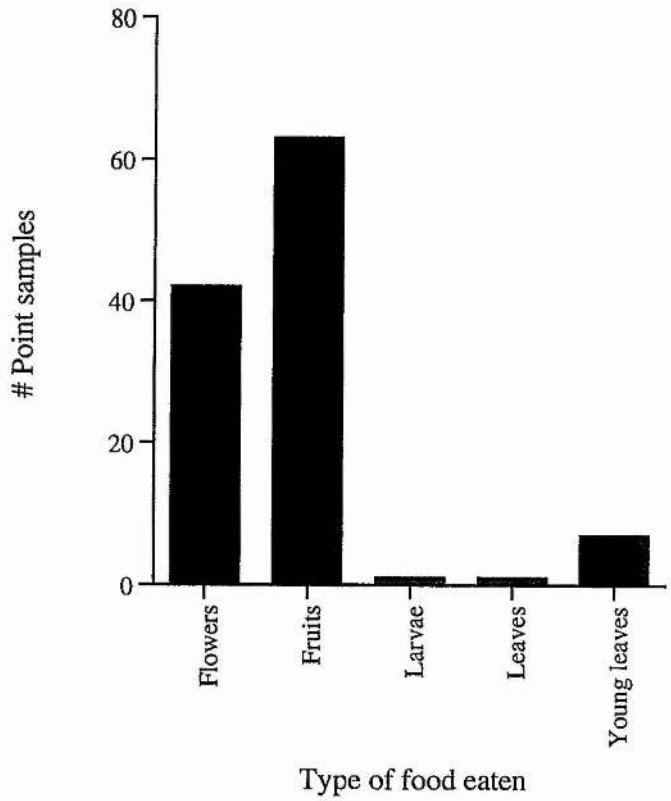


Figure 4.2. Number of point samples in which *whinnies* occurred while eating different food types

Table 4.1. Total number of responses to whinnies given in different contexts

Contexts	Responses		
	No reaction	Give whinny/other call	Approach
FEEDING (N=382)	261	111	10
RESTING (N=102)	95	6	1
LOCATIONAL 1 (N=62)	21	34	7
LOCATIONAL 2 (N=157)	33	117	7
LOCATIONAL 3 (N=183)	46	127	10
OBSER/PRED (N=107)	107	0	0

Table 4.2. Total number of responses to whinnies given in different contexts

(lumping the 3 locational categories)

Contexts	Responses		
	No reaction	Give whinny/other call	Approach
FEEDING (N=382)	261	111	10
RESTING (N=102)	95	6	1
LOCATIONAL (1/2/3) (N=402)	100	278	24

Table 4.3. Partitioning of a 3x3 contingency table (table 4.2.) following Siegel and Castellan 1988

1st Subtable

	Give whinny	Approach
Feeding	111	10
Resting	6	1

non significant

2nd Subtable

	Give whinny + approach	No reaction
Feeding	121	261
Resting	7	95

chi-square=19.84
p<0.001

3rd Subtable

	Give whinny	Approach
Feeding+ resting	117	11
Locational	278	24

non significant

4th Subtable

	Give whinny + approach	No reaction
Feeding+ resting	128	256
Locational	302	100

chi-square=208.3
p<0.001

The first 2x2 subtable compared the responses 'give *whinny* 'and 'approach' in the two contexts, feeding and resting (non significant; chi-square=0.032; df=1; p>0.80). The second one compared those two responses together (active responses) versus 'no reaction' in the same two contexts (feeding and resting). *Whinnies* given in a feeding context provoked active responses significantly more often than resting context's ones (chi-square=19.84; df=1; p<0.001). The third subtable compared the responses 'give *whinny* 'and 'approach' in the contexts feeding and resting taken together, versus a locational context (non significant; chi-square=0.042; df=1; p>0.80). The fourth and last subtable compared the active responses together versus 'no reaction' in feeding and resting contexts together, versus a locational context. *Whinnies* given in a locational context provoked significantly more active responses than those given in feeding or resting contexts (chi-square=208.3; df=1; p<0.001)(see figure 4.3.). Thus, the biggest difference in the original table occured between active/non-active responses in locational contexts compared to the other two contexts.

These are the results of occurrences of *whinnies* from all identified individuals taken together. As mentioned above, the amount of observation time per focal individual was different. However, three chi-square tests were conducted on data from three focal individuals separately (individuals for whom enough data for separate chi-squares was available). After the Bonferroni's correction, a level of significance equal or lower than 0.02 was used. The tests revealed significant differences in the responses of each monkey to *whinnies* given in the three different contexts (adult male: chi-square=28.61; df=2; p<0.001. First adult female: chi-square=46.31; df=2; p<0.001. Second adult female: chi-square=6.02; df=2; p<0.02). The same partitioning procedure as the one explained above (Siegel and Castellan 1988) was applied for each individual to find where the differences really were. For all three monkeys the results of the partitioning method showed that they responded significantly more actively to *whinnies* given in locational rather than feeding or resting contexts (Chi-square=26.23; df=1; p<0.001. Chi-square=4.21; df=1; p<0.02. Chi-square=41.51; df=1; p<0.001).

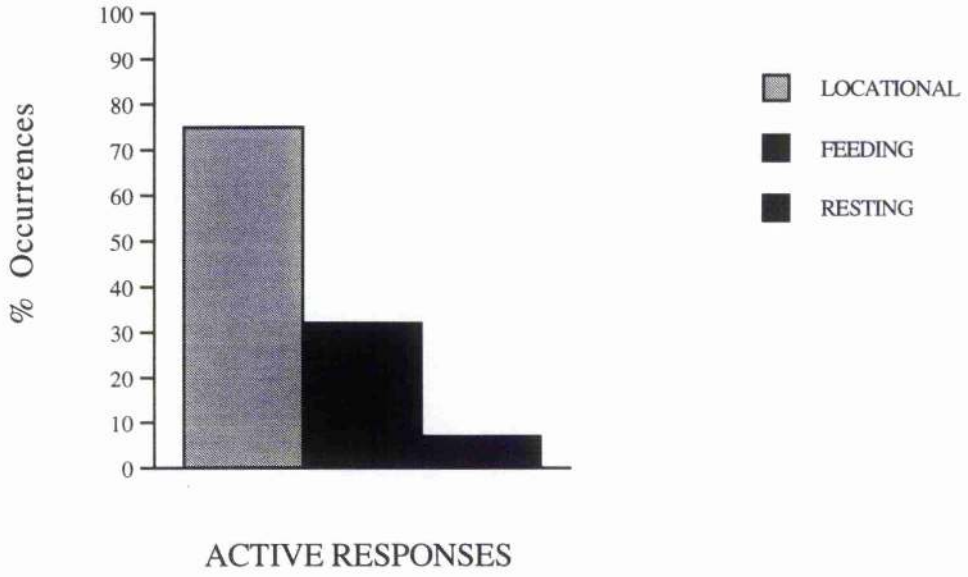


Figure 4.3. Percentage of whinny occurrences in each context after which monkeys gave active responses (i.e. give whinny or approach)

4.1.3. DISCUSSION

The *whinny* occurs in a wide variety of contexts. Here I focussed on four of these contexts and discovered that *whinnies* emitted in each of them elicited different responses from receivers. 'Locational' *whinnies* generally provoked an answering *whinny* call, whereas 'resting' *whinnies* did not; 'feeding' *whinnies* were intermediate. *Whinnies* given by an individual who has seen an observer were never responded to. Given what is known about spider monkey's highly dispersed spatial patterns while feeding or travelling, it seems that the responses given were the most appropriate for each particular situation. When spider monkeys hear a 'locational' *whinny* from an individual who might have lost track of the subgroup in which he was travelling or who is rejoining the subgroup after a period of separation, they *whinny* back, thus informing about their location. Whereas, when they hear a *whinny* from an individual eating or resting they just tend to resume what they were doing, not reacting. However, some locational *whinnies* were not answered, and some feeding *whinnies* were answered by giving *whinnies* back. Why are some of these *whinnies* answered and others not? It may be the case, as suggested in the introduction, that spider monkeys' use of the *whinny* is highly context-specific, and that differences in the responses to *whinnies* occur because they are given in different contexts which provide additional cues to guide the responses of the receivers. However, in many cases the individual emitting the *whinny* was eating in a fruiting tree, out of sight of the receivers, so the call itself must have informed others about either the existence of food or the particular location of a conspecific. Is there some information encoded within the call, besides possible motivational cues, that guides the listener to call back, approach the caller or just ignore the call and continue eating? How would spider monkeys respond if they heard a *whinny* independently of its context? In the next section I describe playback experiments designed to discover what specific information the *whinny* conveys, and if any whether each *whinny* type (locational versus feeding) elicits functionally distinct responses.

4.2. Playback experiments of feeding versus locational *whinnies*

4.2.1. METHODS

Study site

Playback experiments were conducted at Santa Rosa National Park, on the same community of 60 individuals described in the previous section. Because of this species' fission-fusion ranging the experiments had to be carried out as opportunities presented.

Selection and preparation of acoustic material

The calls used were tape-recorded from identified individuals during spontaneous bouts of 'whinnying' in either feeding or locational contexts (as defined in part I of this chapter). Because I rarely contacted adult males in the core area, most of the *whinny* samples were from females. The *whinnies* used for the playbacks were chosen from these natural field recordings and then edited with SoundEdit Pro 1.0. After looking at the spectrograms produced with this program, the ones of best quality and minimum background noise were selected. In order to avoid the pseudoreplication problem (McGregor et al.1992), the samples selected were *whinnies* from different individuals (see table 4.4.). Two tapes with calls given by identified individuals within the community were prepared: one consisting of *whinnies* originally given in feeding contexts, and the other consisting of *whinnies* originally given in locational contexts.

Protocol

Playback trials were conducted from September to November 1994 (wet season). A total of 20 trials were conducted, 10 with *whinnies* given in locational contexts and 10 with *whinnies* given in feeding contexts. Two observers participated in the experiments. I hired a local assistant, who was responsible for setting up the equipment and playing the call. I was in charge of recording the vocal and behavioural responses of the monkeys.

Calls were played through a portable speaker, located in a tree 5 to 12m above the ground (mean=8.3m; SE=0.5m; n=20). A Peavey SOLO Portable sound system, with speaker & amplifier, was used; the frequency response was essentially flat over the frequencies of interest. The speaker was always hidden, and located at a distance of 10 to 150m (mean=41.6m; SE=8.74m; n=20) from the subgroup of animals being tested (see plate 7, speaker hidden in the canopy marked by an orange circle). It was always oriented in the monkeys' direction and connected to a SONY cassette player (WM-EX12) that was controlled by one of the observers at a distance from the speaker of 20 meters.

Table 4.4. Number of trials conducted with each whinny sample in the two types of playback

Type of playback	Individual	Number of trials conducted
LOCATIONAL Whinnies (Santa Rosa)	A.F. NB. WHINNY	3
	A.F. DV. WHINNY	2
	A.F. V. WHINNY	2
	A.F. CR. WHINNY	1
	A.M. M1. WHINNY	1
	Juv.F.WHINNY	1
FEEDING Whinnies (Santa Rosa)	A.F. DNB. WHINNY	3
	A.F. F1. WHINNY	2
	A.F. NB. WHINNY	2
	A.M. M1. WHINNY	1
	Juv.F.WHINNY	1
	Sub.F.WHINNY	1

Table 4.5. Number of trials conducted in each time of day (morning/ afternoon)

	Morning	Afternoon
Locational Whinnies (N=10)	8	2
Feeding Whinnies (N=10)	5	5

Plate 7. Speaker hidden in the canopy in the upper part of the photograph approximately 12m above the ground.

The appropriate volume level was set by estimation, on the basis of natural production levels (these had been determined previously, well away from the monkeys' range, with the speaker at 12m height).

Most trials were conducted either in the early morning between 5.00-6.30am while the animals were still resting in a sleeping site (n=3), or in the late afternon (see table 4.5.). Most active feeding periods took place during the morning, until 11.30am, and late afternoon, between 15.00-17.00pm. If a trial was to be conducted in a sleeping site (n=6), the rope to haul the speaker to playback height was set up the night before the experiment, and the tree in which the speaker would be positioned was marked. Next morning, before dawn (5.00-5.15am), the speaker was hauled into the tree, and the observers waited until there was enough visibility to see the monkeys. If a trial was to be conducted in a fruiting tree while the monkeys were eating (n=6) or resting (n=5), the speaker was either set up beforehand in a tree on which the monkeys were likely to feed that day; or, a fruiting tree in which the monkeys were already feeding was chosen, and one observer monitored the subgroup composition and behaviour of the monkeys, while the other quietly positioned the speaker. Only 6 trials were conducted during group progression from one location to another. In some trials (n=5) we separated and walked through the study area looking for the monkeys; once successful, we contacted one another with a walkie-talkie (Realistic TRC-226 40-channel band transceiver), informing about their location so we could set up for the experiment.

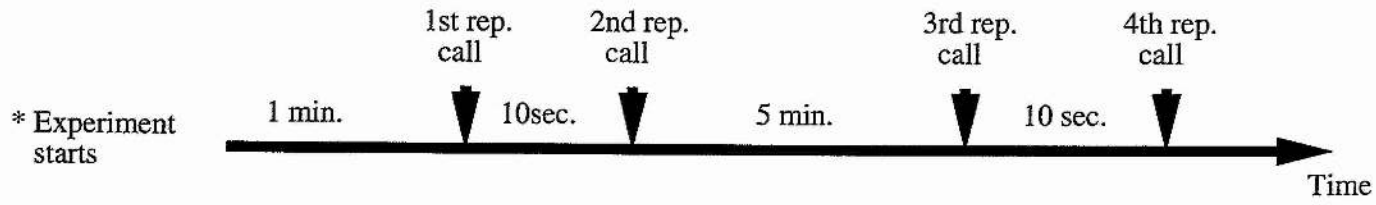
Two conditions had to be met before a trial began:

a) the caller was not among the audience

b) no two trials were ever conducted on the same individual on the same day.

The order in which I conducted a trial with a 'feeding' or a 'locational' *whinny* was randomized. The same call was played four times. Before each trial, one minute of behavioural recording of one monkey was collected. This focal animal was chosen on the basis of its visibility; if the subgroup contained two or more individuals involved in different activities, the activity recorded was that of the individual who was more visible. If during that period of one minute a subgroup of monkeys for example moved away from the site or started a chorus of *whinnies* the trial was terminated. Following this period the call was broadcast once and, after 10 sec., the call was played again; then, there was a 5 min. lapse before the call was played two further times, again with a 10 sec. interval between (see figure 4.4., diagram of experimental design). A 10 sec. interval between repetitions was chosen because it falls within the range in which spontaneous *whinnies* are given (average interval 20 sec; range 0.03 sec - 3 min), but towards the lower part of the range. Using a longer interval could have risked the monkeys moving away from the site. A total of 15 trials had to be aborted because either of the conditions above mentioned could not be met, or because one of the following incidents took place: a chorus of calls or

Figure 4.4. Experimental design



a sudden noise (a car passing nearby) occurred; the monkeys had moved to a different sleeping tree during the night (something common when there was full moon) so we could not find them in the morning; the monkeys never came to the fruiting tree where we had set up for the experiment.

Data collected during trials

The information collected in each trial consisted of the recordings of all calls given in response to the playbacks and a spoken description. A Marantz CP 430 tape recorder and a Sennheiser MKH 816T directional microphone were used to record calls, while verbal comments were spoken into a small tape recorder and transcribed into a written report each evening. Tapes SONY UX.S chrome class were used for the vocal recordings.

Comments included:

General information

* date
* location (noted on map of the study area)
* time the experiment started
* time the experiment finished
* speaker location, height and distance to the monkeys.

Receivers of the call

* approximate subgroup size and composition
* receivers' identities (if known)
* activity the monkeys were involved in (if the subgroup contained two or more individuals involved in different activities, the activity recorded was that of the individual who was more visible):

RESTING: the monkeys were not locomoting and were not engaged in any of the activities named below.

EATING: the monkeys were ingesting and/or foraging for a food item. If known, the species of the tree and part eaten (fruit, leaf or flower) were noted.

MOVING: the monkeys were locomoting from one tree to the other, leaving a sleeping or feeding site or traveling between foraging areas.

Responses to the playback

* time the first individual responded to the playback
* number of individuals vocalizing within 10 min. of the playback start
* total number of calls within 10 min. of playback start.

The gun microphone picked up the calls of all subgroup members, enabling accurate counting (though not assigment to particular individuals) of calls made in response to the playback. The behaviour given was scored using pre-defined behavioural categories.

Behavioural categories were selected for scoring on the basis of previous observations of responses to spontaneous use of these calls:

* **Look speaker**: the animal changes the position of its head, orienting it towards the speaker.
* **Scan**: an individual is in an alert position, lifting its head up but not looking in the direction of the speaker.
* **Approach speaker**: locomote towards the area or tree where the speaker is located.
* **Give *whinny*.**
* **Give other type of call** (*squeals, barks, or long calls).*

The latency to respond was measured from the first time the call was played. Although the data analyzed only included responses occurring during the 10 min. after the last time the call was played, the monkeys' behaviour was recorded for an hour.

4.2.2. RESULTS

One of the main findings of the experiment showed that there was a difference in the response 'scan', after hearing the two types of *whinnies*. Spider monkeys scanned more often after hearing feeding rather than locational *whinnies* (Fisher Exact Probability Test, p=0.03; I used this test to compare the number of trials in which different responses were given to the playbacks of the two distinct *whinnies*; see table 4.6.). Although there was a trend for monkeys to 'give *whinnies*' after locational rather than feeding *whinny* trials, this was not significant (Fisher Exact, p=0.08). In other ways the responses to both types of *whinnies* were similar and did not occur in more trials of one type rather than the other (Fisher Exact, 'look speaker' p=0.33; 'approach' p=0.5). The monkeys did not give any other type of call after the playbacks.

There were no significant differences in the amount of calling or in the number of respondents when locational versus feeding *whinnies* were played. The total number of calls given to the two types of playback did not differ (Mann-Whitney test on total number of calls, W=125; p=0.11; adjusted for ties), and nor did the number of individuals responding (W=127; p=0.10; adjusted for ties)(see table 4.7.).

Table 4.6. Number of trials in which different responses were given to the 2 distinct whinnies

	Responses			
	Look speaker	Scan	Approach	Give whinny
Locational whinnies (10 trials)	6	2	1	7
Feeding whinnies (10 trials)	7	8	1	3

Table 4.7. Effect of subgroup size, activity, location, sex of the caller and time of day on calling behaviour

Total trials=20

	TRIAL #	DATE	TIME DAY	SLEEP SITE	SUBGROUP SIZE	ACTIVITY	TOTAL CALLS	N.INDIV RESP.	LATENCY
LOCATIONAL WHINNIES	1	13/9/94	morning	Y	5	moving	2	2	6sec
	2	24/9/94	morning	Y	1	resting	2	1	5sec
	3	6/10/94	morning	N	6	eating	6	4	4sec
	4	20/10/94	afternoon	N	3	eating	1	1	8sec
	5	2/11/94	morning	Y	2	moving	0	0	_
	6	3/11/94	afternoon	N	2	eating	5	3	2sec
	7	11/11/94	morning	Y	3	resting	1	1	6sec
	8	22/11/94	morning	Y	5	moving	3	3	3sec
	9	22/11/94	morning	N	2	resting	0	0	_
	10	11/10/94	morning	N	2	moving	0	0	_
FEEDING WHINNIES	1	13/9/94	morning	N	3	resting	0	0	_
	2	30/9/94	morning	N	3	eating	0	0	_
	3	4/10/94	morning	N	10	eating	0	0	_
	4	19/10/94	afternoon	N	3	resting	3	2	3sec
	5	19/10/94	afternoon	N	3	eating	4	2	5sec
	6	8/11/94	morning	Y	4	resting	0	0	_
	7	15/11/94	afternoon	N	2	resting	0	0	_
	8	18/11/94	afternoon	N	2	resting	1	1	8sec
	9	18/11/94	afternoon	N	5	moving	0	0	_
	10	21/11/94	morning	N	4	moving	0	0	_

There were no significant differences in the latency to give a call after the two types of playback (W=37.5; p=0.91; adjusted for ties).

In the following analyses which examine the effects of various independent variables on monkeys' reactions to playbacks, the latency to respond and the frequency of vocalizing are analyzed systematically, but other response categories were often used too infrequently for statistical treatment to be possible; all cases that could be tested are presented below.

Subgroup size may affect the level of feeding competition and thus the response of a spider monkey when hearing a feeding or a locational *whinny*. In order to investigate the effect of subgroup size on the vocal responses of the monkeys, target subgroups were divided into three categories: small (1-3 individuals); medium (4-5); large (more than 5)(table 4.7.). In playbacks of feeding *whinnies*, the only trials in which calling occurred were when a small subgroup was receiving the call, so no test could be applied. In playbacks of locational *whinnies*, the subgroup size had no significant effect on the number of individuals responding (H=1.25; df=2; p=0.54, Kruskall-Wallis test, adjusted for ties) or on the latency to respond (H=0.37; df=2; p=0.83). (Note that, since the probability of a call eliciting a response in the audience depends on the number of individuals which can potentially respond, the raw frequencies would be misleading: the number of individuals responding was divided by the number present who could potentially respond, and these data used in the tests). No test could be performed on any of the behavioural responses because they occurred at too low frequencies (chi-square test cannot be used when more than 20 percent of the cells have expected frequencies of less than 5; Fisher Exact was not used because it can only be used on a 2x2 contingency table).

The activity or context the monkeys were involved in while hearing the playback might influence their responses to the playback of feeding and locational *whinnies*. No such effect was found, either on the calling frequency, the number of individuals responding or on the latency to respond. Kruskall-Wallis tests, adjusted for ties, were performed on the total number of calls given, the number of individuals responding and on the latency to respond, in the three different activities in which they were involved during playbacks: moving, resting and eating (table 4.7.). No significant difference emerged with locational *whinnies'* playbacks (H=2.7; df=2; p=0.265. H=2.64; df=2; p=0.27. H=0.35; df=2; p=0.84, respectively). No tests could be conducted on feeding *whinnies'* playbacks because the sample was too small. Not enough data were available to investigate the effect of activity on the behavioural responses given.

Arousal also varies with time of day, since there are different peaks of activity in the course of the day (e.g. spider monkeys' peak of feeding takes place in the early morning and late afternoon). But once again, no effect of this variable (morning or afternoon) was noted. The total number of calls given, number of individuals responding and latency to

respond to the playbacks of locational *whinnies* did not vary with time of day (Mann-Whitney adjusted for ties, W=41.5; p=0.59; W=41.5; p=0.59; W=20; p=1, respectively). This test could not be applied to playbacks of feeding *whinnies* because all calling occurred in the afternoon. The responses give *whinny*, look speaker and scan in either type of playback, all failed to show a time of day effect (locational: Fisher Exact p=0.47; p=0.66; p=0.62, respectively. Feeding: Fisher Exact p=0.083; p=0.50; p=0.78).

The fact of conducting a trial in a sleeping site, where the monkeys are generally resting but vigilant, or in a feeding tree, where they are busy eating and less vigilant, could have affected their responses to playbacks. However, the location where a trial was conducted (in a sleeping site or in a feeding tree) had no effect on the total number of calls given to playback of locational *whinnies* or on either the number of individuals responding, or the latency to respond (Mann-Whitney adjusted for ties; W=27.5; p= 0.1; W=27.5; p=1; W=17; p=0.86, respectively). There were no significant differences in the responses give *whinny*, look speaker or scan to playbacks in either location (Fisher Exact, p=0.5; p=0.74; p=0.78). There were not enough data in feeding *whinnies*' playbacks to test the effect of location (only one trial of a playback with a feeding *whinny* was conducted in a sleeping tree, with no response from receivers; see table 4.7.).

GENERAL DISCUSSION

The results of playback experiments showed that *whinny* calls recorded in two different circumstances transmitted different information to conspecifics, without requiring contextual cues. There are, then, at least two types of *whinny*: a 'feeding' and a 'locational' one. Although the responses given to the two types were not dramatically different, spider monkeys did respond more actively to locational *whinnies* by 'whinnying' back, whereas they scanned more when they heard feeding *whinnies*. If locational *whinnies* do function as position indicators, these results would make sense because the monkeys were informing the caller about their location by 'whinnying' back. Moreover, if the feeding *whinny* is a referential call that informs other monkeys about the location or quantity of food (as Chapman and Lefebvre 1990 suggested), then the scanning behaviour when hearing *whinnies* may be a way of locating potential feeding sites.

Although the independent variables measured (the size of the subgroup hearing the call, the activity in which the receivers were involved, the location and time of day of the broadcast) had no effect on the response rate, one still has to rule out the possibility that particular acoustic features of the stimuli used in the playbacks or the fidelity of the equipment did not influence the results. The most likely to affect the fidelity of sound

production are the duration of the calls used and the distance of the speaker during playbacks.

The average duration of the *whinny* is 0.90sec although there is much variability between calls (0.30-2.00sec) (Chapman & Weary 1990). The duration of a call is a feature which may affect the response of an individual. The length of the *whinnies* selected for the playbacks varied between 0.74 and 1.78 sec. In order to test if there was an effect of call length in the monkeys' responses I divided all durations into three categories: long (1.00-2.00 sec.), medium (0.65-1.00 sec.) and short (0.30-0.65 sec.). With locational *whinnies* 'playbacks, the duration of the *whinny* had no effect on the total number of calls given or on the latency to respond (Kruskall-Wallis adjusted for ties; H=3.73; df=2; p=0.15. H=0.65; df=2; p=0.72)(see table 4.8a). No test could be performed on the behavioral responses because they occurred at too low frequencies. With feeding *whinnies* 'playbacks, only medium length calls elicited calling, so a Kruskal-Wallis test could not be used to compare latency or call numbers (see table 4.8b.). However, responses such as 'look at the speaker' or 'scan' were observed with calls of all lengths, and here a Fisher Exact test showed no difference between medium and all other length calls (all non significant).

According to Eisenberg (1976), *whinnies* are calls that promote contact in the forest while feeding but do not carry far (he did not specify any particular distance). In Santa Rosa dry forest, when there was no wind we could hear the *whinnies* from distances up to approximately 150-200m in a direct line. The distance at which the monkeys heard the playback calls could have affected the perceived loudness at which the calls were heard and thus their responses to them. In order to test if the distance at which the monkeys heard the *whinnies* played affected the calling behaviour or the latency to respond, I divided all the distances into 3 categories (approximate distances): nearby (10-40m), medium (40-75m), distant (more than 75m away). A Kruskall-Wallis test on the number of calls given in locational *whinnies*' playbacks showed that the distance at which the speaker was located had no significant effect on the number of calls produced (H=0.96; df=2; p=0.62), nor on the latency to respond (H=0.82; df=2; p=0.66)(see table 4.8b). No test could be performed on the behavioral responses because they occurred at too low frequencies. In feeding *whinnies* 'playbacks there were not enough calls given in response to investigate the effect of distance.

Table 4.8. Relationship between the duration of the playback call and the hearers' reaction

4.8a. Locational whinnies

Whinny sample	Duration (msc)	Number of calls given
AF NB 3.77 (3 trials)	816.7	2
	"	2
	"	5
AF D.Viejita (2 trials)	1380.3	6
	"	1
AF Viejita (2 trials)	733.3	0
	"	1
AM M1 (1 trial)	782.2	0
AF Collar Rosa (1 trial)	1368.9	3
Juv F (F1)	1426.4	0

4.8b. Feeding whinnies

Whinny sample	Duration (msc)	Number of calls given
AF DNB 2.58 (3 trials)	1299.9 (L)	0
	"	0
	"	0
AF NB 2.57 (2 trials)	989.3 (M)	3
	"	4
AF F1 (2 trials)	742 (S)	0
	"	0
Juv F (F1) (1 trial) 0.04	926 (M)	1
Suba. F? 1 trial 2.39	1777.3 (L)	0
AM M1 (1 trial)	1276.9 (L)	0

Thus, spider monkeys do genuinely seem able to discriminate between locational and feeding *whinnies* on the basis of hearing these calls without apparent contextual cues present. However, why were there some cases in which monkeys called back to feeding *whinnies,* and others in which they did not respond to locational *whinnies* in the playback experiments? It seems that there was not a complete specificity of response, as is apparently the case with vervet monkeys' alarm calls and rhesus macaques' screams (Marler et al. 1992). In playbacks of these species' calls the signal alone encoded sufficient information about referent characteristics to allow conspecific receivers to respond appropriately. In the case of the *whinny,* there may be two possible explanations for the lack of specificity of response: one is that the *whinny* may allow a wider margin of error in the specificity of response because it is less costly to respond inadequately to a feeding or contact call than to an alarm call; the other explanation is that responses to *whinnies* may be more subtle, not as salient and opposed as responses to alarm calls are. The receivers might have responded with a change in the direction of gaze, difficult to measure in such an arboreal species under observational conditions.

By looking at the results of the two parts of this chapter together, one can conclude that spider monkeys' *whinnies* given in different contexts elicit different responses from conspecifics. There are at least two functionally different *whinnies*, a locational and a feeding one. However, the information conveyed by these two calls and the degree of referentiality they possess is a somewhat more obscure question. On the one hand, these two *whinnies* would not fulfil the 'production specificity' criterion used by Macedonia and Evans (1993)(see Introduction, chapter 1) according to which referential signals should exhibit a high degree of stimulus specificity. For example, the 'feeding' *whinny* is given when finding food of varied types (fruit, leaves, flowers) and different quantities (a fig tree full of ripe fruit or a small tree with scattered favoured flowers), and the 'locational' *whinny* is given in varied social situations. On the other hand, as Marler et al. (1992) suggested for other primate calls (i.e. vervet monkeys' grunts), 'feeding' and 'locational' *whinnies* may occupy an intermediate position on a motivational-referential continuum, most examples having both components. While not determined entirely by the sender's motivational state (as implied in Klein's 1972 conclusion and in Eisenberg's 1976 work), these two types of *whinny* do seem to lack the degree of referential specificity that other primate calls such as vervet alarm barks have (Seyfarth et al. 1980). Thus, the feeding *whinny* could be a generalized call associated with environmental referents (food, drink or a safe sleeping site), having the potential ability to inform others about food abundance by changing for example the rate with which is given (as suggested by Chapman and Lefebvre 1990, although not proved with playback experiments). Whereas the locational *whinny* could be associated with social referents (a juvenile individual lost, an infant needing care, an individual joining a subgroup, etc...).

Finally, one of the limitations that this study of the use of the *whinny* may have is that I only focused on the function and meaning of two types of *whinny*. However, I described in the first part of my study that other *whinnies* such as 'resting' *whinnies* provoked different responses from receivers. Playback experiments would be necessary to demonstrate the specificity of responses of these calls and the degree of referentiality they possess.

In this chapter spider monkeys responded differently to different *whinnies* even though the experiments were carried out in a variety of social circumstances. This suggests that the 'meaning' of each *whinny* may depend to a large extent on the acoustic properties of the call itself rather than on the context in which it is given. In the next chapter I investigate a number of acoustic cues which spider monkeys might use to distinguish between feeding, locational and resting *whinnies* and respond differently to them.

Chapter 5
Acoustic analysis of *whinnies*: individual and contextual variation

5.1. INTRODUCTION

As time passed during my study of spider monkeys at Santa Rosa National Park, and I had more experience with the monkeys' vocal behaviour and ranging habits, I became aware of the large number of different individuals a particular adult female would encounter and maintain vocal contact with in a single day. Like most primatologists who study primates living in social groups, I considered as obvious the fact that spider monkeys must be able to recognize each other by voice alone. I observed that after spontaneous emissions of *whinnies* the monkeys responded differently to calls of different individuals. For example, an adult female may give a *whinny* in reply to her juvenile son's *whinny* and approach him, while she may ignore completely the *whinny* of another adult female, not even looking at her.

Individual vocal recognition is a widespread phenomenon among primates but also among other mammals and birds (Green and Marler 1979). When approaching the issue of primate vocal individual recognition studies have focused on two aspects. One is concern with whether there is significant acoustical variation among the same type of calls of different individuals to support recognition in principle. The other refers to demonstrating, through playback experiments, that primates respond differently to the calls of different individuals, thus showing that individual recognition does in practice take place. Although individual variation in acoustic features is a prerequisite for individual recognition, its occurrence does not always imply that recognition also occurs because primates may not pay attention to the variations found in sound analysis (Falls 1982). A few examples of studies that have shown the existence of individual variation in the acoustic structure of vocalizations of both New World and Old World primates are: Marler and Hobbett (1975) found individual differences in some acoustic variables of chimpanzees' (*Pan troglodytes*) long-range calls, 'pant-hoots'; Lillehei and Snowdon (1978) proved that individual differences existed in the 'coo' vocalizations of young stumptail macaques (*Macaca aractoides*); Smith et al. (1982) demonstrated individual differences in the 'isolation peep' and the 'chuck call' of squirrel monkeys (*Saimiri sciureus*). Other studies have shown through playback experiments that in addition to consistent differences between the calls of different individuals, animals also respond selectively to the calls of certain individuals. Snowdon and Cleveland (1980)

demonstrated distinct individual features of two contact calls, the closed-mouth 'trills' and 'J-calls', and individual recognition of familiar individuals' 'J-calls' in pygmy marmosets (*Cebuella pygmaea*). Playback studies have also shown that females and infants recognize each others' calls, i.e. adult female vervet monkeys (*Cercopithecus aethiops*) can discriminate their offspring's screams from those of other inmatures (Cheney and Seyfarth 1980). Finally, although working with a small sample size (3 subjects), Bauer and Philip (1983) showed that chimpanzees have the ability to recognize familiar long-distance vocalizations and facial configurations, matching the playback of a pant-hoot vocalization of a familiar individual with a picture of the face of that individual.

In the case of spider monkeys, Chapman and Weary (1990), working in Santa Rosa National Park on the same population as the present study, found consistent acoustic differences between the *whinnies* of different individuals. Out of the six acoustic variables measured, three of them differed significantly between individuals. Although they did not conduct playback experiments, their results show that within the *whinny* there is potential for individual vocal recognition. In this chapter I will attempt to replicate this finding of sufficient variation between individuals' *whinnies* to allow the discrimination of each monkey.

In the previous chapter I showed through quantitative analysis of behavioural responses to *whinnies* and playback experiments that spider monkeys use at least three different types of *whinnies*, feeding, locational and resting variants, to which monkeys give functionally different responses. A second aim in this chapter is to find out if these three types of *whinnies* are acoustically different. Although to my human ear there are no immediatlely obvious audible differences among the three *whinny* variants, there seems to be enough acoustic information in these calls for receivers to discern what the appropriate responses to each of them are. No attempt has been made so far to discriminate acoustically between *whinnies* given in different contexts. Eisenberg (1976) described an extensive call variability in spider monkey's (*Ateles fuscipes*) vocal repertoire, and recognized several subcategories for the *whinny* on the basis of its acoustic structure alone (see methods below). Chapman and Weary (1990) described individual differences in only one context (feeding); they did not consider other potential sources of acoustic variation besides individual differences. A second aim in this chapter is to find out if these different types of *whinnies* are acoustically different.

This phenomenon could be a case of 'phonetic variability' (see Introduction). A result that has arisen in several studies of primate vocal communication is the existence of calls which sound similar, appear to belong to a unitary call type and have a general function, but in fact have several variations, specific to a single context, and each with a distinct acoustic structure: Green 1975, Japanese macaques' coos; Cleveland and Snowdon 1982, cotton-top tamarins' calls; Cheney and Seyfarth 1982, vervet monkeys' grunts; Snowdon et al. 1983, cotton-top tamarins' long calls. For example, Cheney and Seyfarth (1982)

proved through the use of playback experiments that vervet monkeys have four different types of 'grunts' to which monkeys respond differently, and found a number of distinct acoustic features across individuals and grunt types by which grunts could potentially be distinguished from each other.

To accomplish the two aims exposed above I will first analyze the structural differences of *whinnies* quantitatively. I will measure several acoustic features to discover which differentiates each monkey's call from that of every other individual. In the same way, I will analyze quantitatively the structural differences of two types of *whinnies* (feeding and locational) to find out which features differentiate each *whinny* type from the other and how effectively.

5.2. METHODS

Call description

The first and most detailed acoustic description of the *whinny* was provided by Eisenberg (1976) in his work on the communication mechanisms of *Ateles*. The main point he stressed was that the vocal repertoire of spider monkeys is a graded system in which the morphology of calls is greatly influenced by the motivational state of the sender. According to him, spider monkey's calls cannot be easily categorized into discrete classes, but rather call structures intergrade with one another along a motivational continuum. He described three variants of the *whinny*: the *slow whinny*, the *tee-tee* and the *true whinny*. The last two were included in a category of high frequency calls with extensive frequency modulation. The *slow whinny* was classified as a call with variable frequencies emphasized. According to this author the contexts in which these three types of *whinnies* were given and their acoustical description were as follows:

a) The *tee-tee*: 'is a high intensity, rapid, nonrepetitive call, used as a greeting call to group members and while feeding' (Eisenberg 1976). Generally less than 0.9 sec. in duration, with an average maximum fundamental frequency of 3.2 KHz and a minimum of 1.2 KHz.

b) The *true whinny*: is similar to the *tee-tee* in structure but longer (may exceed 2 seconds), with an average duration of 0.95 sec. Associated with feeding but also with contact maintenance, group movement and onset of rain. It has an average maximum frequency of 5.2 KHz and minimum of 1-2 KHz.

c) The *slow whinny*: is associated with feeding or when approaching a 'crying' infant. It has an average duration of 2.3 sec., a maximum frequency of 3 KHz and minimum of 0.2-0.7 KHz. This call may grade into the true *whinny*.

Most of the *whinnies* analyzed in this study belong to the first two variants described by Eisenberg (1976). During the field period I carried out a visual inspection of a number of *whinny* sonograms with the sound program SOUND EDIT Pro1.0. A search for the common features of these calls showed that the *whinny* is a tonal call shaped into rising and falling linked arches or elements (range 2-12 elements; mean=6), and that it has a variable number of harmonics (mean=2), occasionally with a noisy component (in a few cases there is a noisy part at the begining of the call or at the base of the arches). The most salient aspect of the call is however the extensive variation in its structure. Figures 5.1. and 5.2. present various examples of sonograms of *whinnies* recorded at the beginning of the study from different individuals, in different contexts.

Study area and subjects

During the period of February to October 1994 I recorded vocalizations of spider monkeys in Santa Rosa National Park, Costa Rica. Recordings were made in both the dry and wet seasons in all types of habitat present in the animals' home range: patches of evergreen riparian forest, deciduous forest, secondary forest and mixed forest (see also chapter 2, study site).

One of the calls I focussed on was the *whinny*. *Whinnies* were tape-recorded from identified and unidentified individual spider monkeys belonging to a community of 60 monkeys. For most of the acoustical analysis only *whinnies* from identified individuals are considered. These come from 10 adult females, a subadult female, an adult male, a subadult male and three juveniles (offspring of the previous females). However, because I did not have enough calls from each of them, only calls from five adult females, a subadult female, an adult male and three juveniles are used here, since their call sample size was appropriate for statistical analyses.

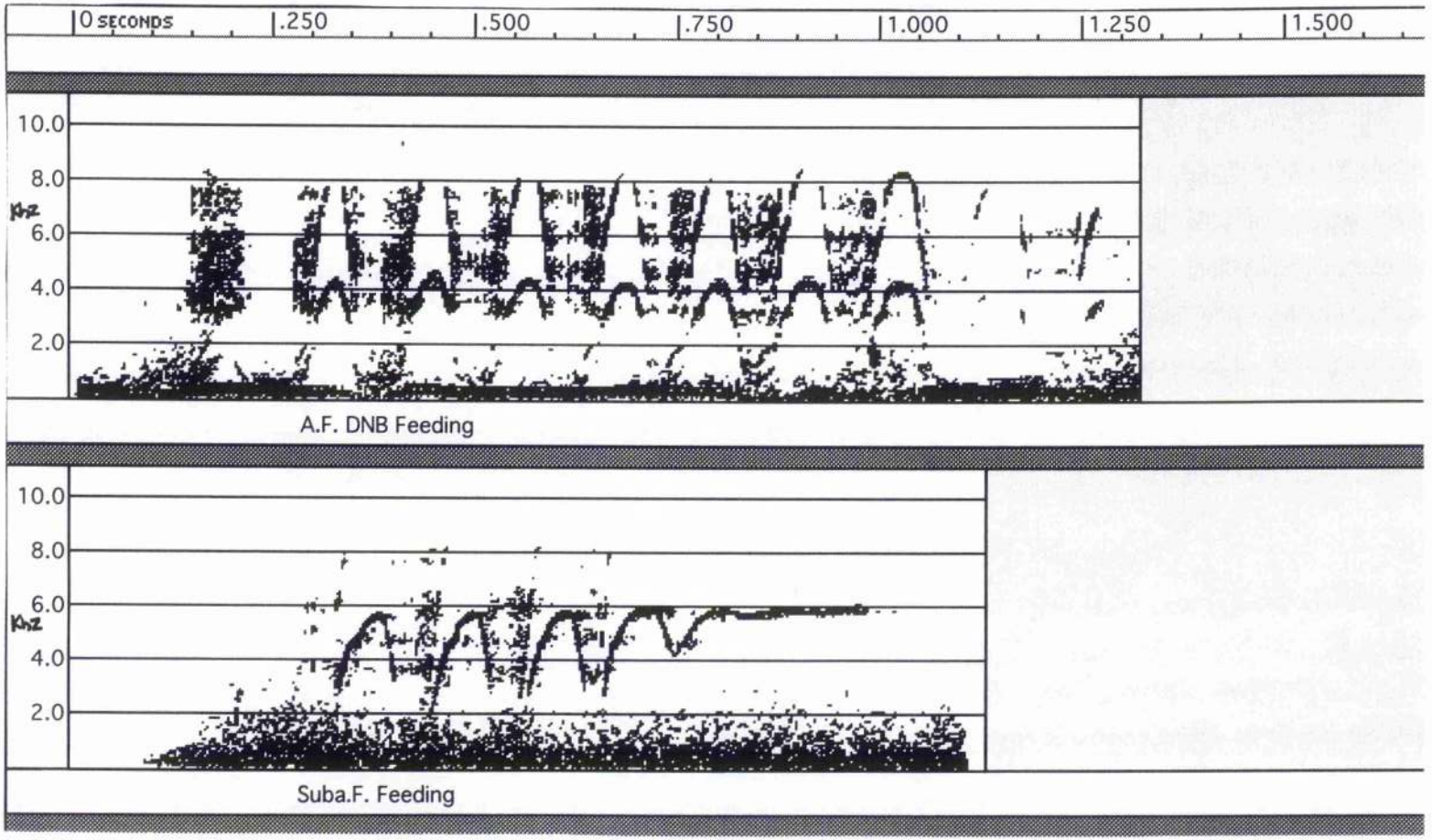


Figure 5.1. Sonograms of *whinnies* of two spider monkey females in the context of feeding.

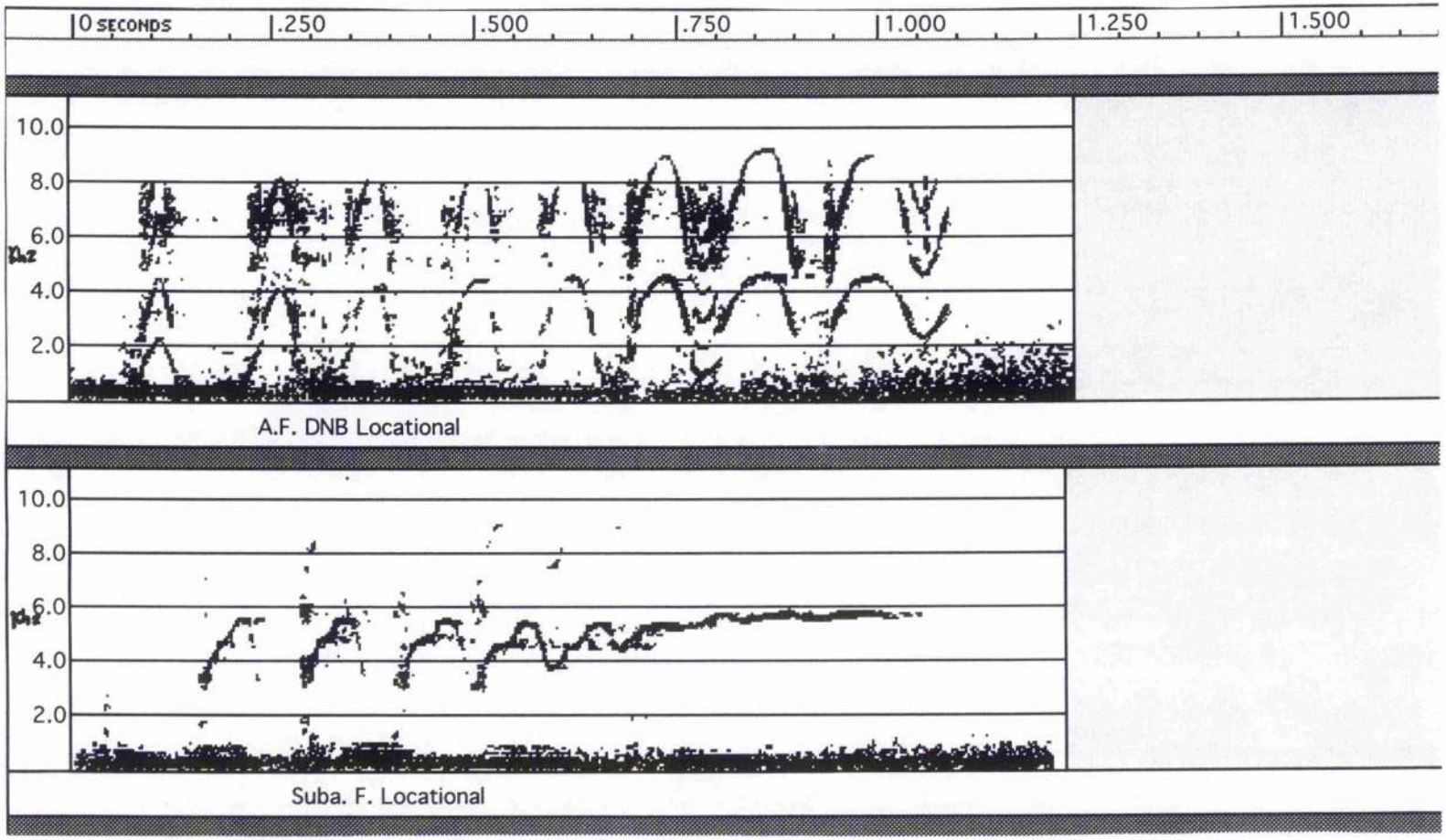


Figure 5.2. Sonograms of *whinnies* of two spider monkey females in a locational context.

Behavioral analysis and call sample

Tape recordings of *whinnies* and behavioural information about the context surrounding the emission of each call and the receivers' responses were made by myself. The contexts explored as potential sources of acoustic variation were: feeding or foraging, resting and a locational context. A locational context was defined as one in which an individual was entering a tree for the first time (a fruiting or sleeping tree), was joining a new subgroup, or had lost sight of the members of the subgroup with which it was travelling (see chapter 4, section 4.1.).

Vocalizations were recorded using a Marantz CP 430 tape recorder, chrome tapes, and a Sennheiser MKH 816T directional microphone with a wind screen. The approximate distance at which vocalizations were recorded varied between 10-30m. Two common places from which I recorded *whinnies* were the base of fruiting and sleeping trees (at both times of day, morning and afternoon). In addition, comments on the behavioural context were described into a clip microphone, recorded on the other channel of the Marantz tape-recorder, and transcribed onto check sheets.

Vocal recording sessions lasted between 20 min and 5 hours, during which *whinnies* were taped with an *ad libitum* sampling technique. The procedure I followed to avoid missing out calls and wasting tape space was to leave the tape recorder on for a set amount of time (i.e. five minutes); if no calls were given during this time I rewound the tape to the starting point (using the counter of the tape recorder). After the emission of a *whinny* I described the identity of the caller, the activity it was involved in, the size and composition of the subgroup it was travelling with, and the behaviour of the listeners of the call (i.e. give a *whinny* back, approach or no reaction). If the caller was eating, I registered the tree species, the DBH (diameter at breast height) and the canopy radius. When a chorus of *whinnies* occurred in a fruiting tree, I did not record them because it was difficult to isolate each individual's call.

The initial data set included 291 *whinnies* (167 given in a feeding context, 35 in a resting context and 89 in a locational one) from 32 individuals (both identified and unidentified). The final data set, however, only included 209 *whinnies* from identified individuals for which I had collected contextual information, and of which the quality of the sonograms was good enough for the acoustic parameters to be measured (i.e. with little background noise). Since the number of *whinnies* per identified individual in each of the sub-categories of locational contexts was not big enough for statistical analyses to be conducted, I decided to lump them into a single category (locational). For the analysis I needed a sample size appropriate for comparing the acoustical characteristics of *whinnies* given in different contexts while simultaneously controlling for individual variation (Lillehei and Snowdon 1978). *Whinnies* given in resting contexts were only analyzed for

one female for which the sample was big enough. Table 5.1. presents a summary of the data set used for each statistical analysis.

Acoustic analysis

The acoustic analysis of *whinnies* was carried out with a Kay 5500 DSP sonograph on a two screen spectographic display. Before I calculated sonograms, the calls were low-pass filtered at 80 Hz and high-pass filtered at 16 KHz because the frequency range of the *whinny* falls within these values. Using a 100-pt Fast Fourier Transform (FFT; weighting function: Hamming window*) in the lower screen and a 512-pt in the upper one, this set-up provided a frequency resolution of 300 Hz and a temporal resolution of 50 ms (lower screen), and a frequency resolution of 59 Hz and a temporal one of 200 ms (upper screen). Only the number of frequency modulations of the call was measured in the lower screen while all the other parameters chosen were measured in the upper screen. All measurements were entered into an Excel 2.1 spreadsheet on a Macintosh PowerBook 145 for statistical analysis.

There is a large amount of acoustic parameters one can measure. The decision of which acoustic parameters to measure was based on the following considerations:

a) Parameters had to be reasonably immune to habitat degradation (e.g. bandwidth of the call was thus rejected).

b) Amplitude measurements were not selected for analysis since when recording freely moving monkeys the distance at which the microphone is or habitat degradation can not always be controlled.

c) A larger number of temporal rather than spectral parameters was selected because previous studies have found temporal parameters to be important sources of variation between individuals (Chapman & Weary 1990; spider monkeys' *whinnies*) and between calls given in different contexts (Hauser 1991; rhesus macaques' 'coos'). Furthermore, during the preliminary period of data collection on *whinnies* the only immediately obvious audible difference I could detect between *whinnies* given in feeding versus locational contexts was that locational *whinnies* were of longer duration and had a higher pitch.

Table 5.2. presents a description of the 11 acoustic parameters that were measured, four spectral and seven temporal features, with the abbreviations that will be used from now onwards in the chapter. The start of the silent interval after the call (INTA) is defined by the time the call finishes to the time the next call (a *whinny* or other) begins. A bout

* Hamming window: the Fourier Transform requires that we delimit a segment of the time signal to be transformed. This is a type of transform window, named after its discoverer.

was considered independent from another if it occurred after more than 5 minutes. Figure 5.3. shows a sonogram of a *whinny* with various acoustic parameters indicated.

Statistical analysis

Statistical analysis concentrated on two aspects of the acoustics of *whinnies*: individual variability and contextual variability. Following Pimentel & Frey (1978) and Falls (1982), acoustical parameters were first examined using ANOVA. ANOVA quantifies the number of features with significant interindividual or intercontextual variation, showing the extent of such variation by the magnitude of the F-ratio. After consulting with Dr. Alan Gordon (Statistics Division of the Department of Mathematical and Computational Sciences, University of St Andrews) a two-way ANOVA was used for comparisons of F-ratios: one factor (individuals) with nine subjects, the other (contexts) with two distinct contexts (feeding/locational). The program used to carry out this two-way ANOVA was GLIM (Generalised Linear Interactive Modelling) which allows a different number of observations for each cell. A total of 10 different ANOVAs were performed, one on each acoustic parameter. Since not all acoustic parameters were normally distributed (Kolmogorov-Smirnoff (Lilliefors) test, $p<0.05$) and none fulfilled the assumption of homogeneity of variances (Cochran test, $p<0.05$), I minimized this problem when possible by using data transformations in several tests (n=3; square root and logarithm)(Tabachnik and Fidell 1989; pp. 86, suggest the square root transformation for this type of skewness). The same transformations (and 'arcos') were used in the remaining tests with no success in normalizing the data or making the variances more homogeneous. However, ANOVA is robust to violation of the normality assumption and after plotting the data only a moderate positive skewness was detected.

Multivariate statistics were also used to assess the percentage of calls that could be classified as belonging to the correct individual or context, based on the call parameters measured. Discriminant function analysis assumes that groups are pre-specified and seeks linear combinations of variables that discriminate between these groups. Applied to these data, it enables reduction of the number of acoustic parameters and creates a number of functions which can be used to classify individual cases (calls) into groups (individuals or contexts); it has been successfully used to discriminate calls of non-human primates on the basis of individual and contextual variation (e.g. Snowdon et al. 1983; Gouzoules and Gouzoules 1989; Hauser 1991). All discriminant analyses were run with SPSS 6.1 following the method described by Tabachnik and Fidell (1989) for direct discriminant function analysis. In contrast to stepwise discriminant function analysis, in the standard (direct) procedure 'all predictors enter the equations at once and each predictor is assigned only the unique association it has with groups. Variance shared among predictors contributes to the total relationship, but not to any one predictor' (Tabachnik and Fidell 1989).

Table 5.1. Data set for statistical analysis of whinnies by context and by individual

Type of Statistical analysis	Number of subjects	Range of calls/subject	Total number of calls
Two-way ANOVA (individuals/contexts)	9	4 - 10	139
Discriminant function analysis (individual differences in a feeding context)	8	10- 33	125
Discriminant function analysis (contextual differences)	9	3- 5	88
3 Discriminant function analyses (within subjects, between contexts)	3	10- 33	111

Table 5.2. Description of the acoustic parameters measured

1. Duration: length of the call (D)
2. Number of frequency modulations in the fundamental (Fo): one modulation=one rising and falling segment of the call (#FM)
3. Duration of first modulation: length of the first rising and falling segment (D1st)
4. Duration of middle modulation: length of the middle rising and falling segment (DM) *
5. Duration of last modulation: length of the last rising and falling segment (DL)
6. Maximum frequency (Fo): maximum frequency of the fundamental (MXF)
7. Minimum frequency (Fo): minimum frequency of the fundamental (MNF)
8. Frequency range: fundamental frequency bandwidth (max-min) (FR)
9. Maximum frequency location: measured from the start of the call (MXFL)
10. Minimum frequency location: measured from the start of the call (MNFL)
11. Silent inter-call interval after the call (INTA)

* If the call had an odd number of modulations the one closest to the middle but occurring first was selected (as described in Chapman & Weary 1990)

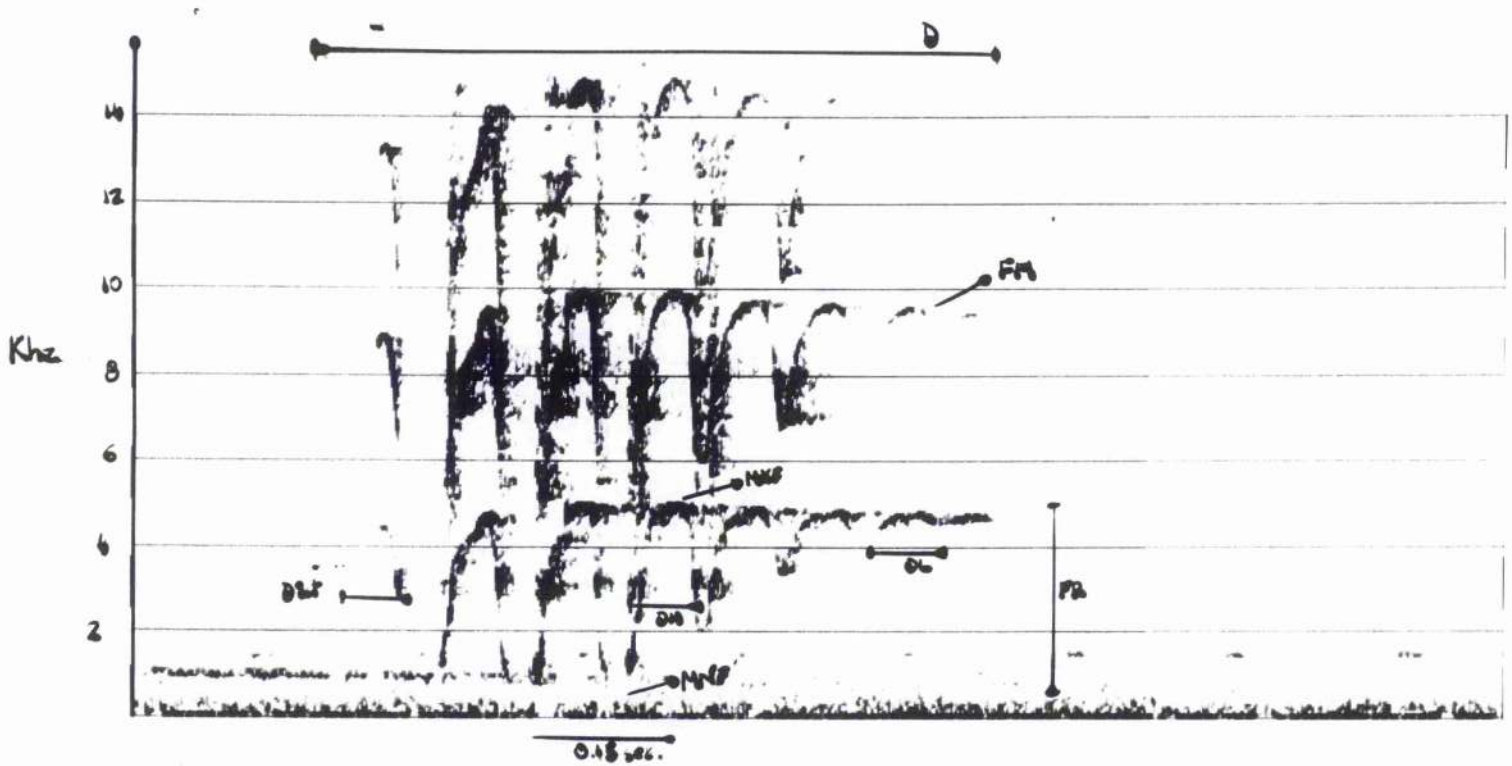


Figure 5.3. Sonogram of a *whinny* given by a juvenile female while resting (date 8-9-94); various acoustic parameters measured are indicated. (Duration of call: 0.95sec. Number of frequency modulations: 7).

In stepwise discriminant function analysis it is statistical criteria that determine the order of entry of predictors. Stepwise discriminant analysis has the same controversial aspects as stepwise multiple regression, i.e. it may overfit the data and the order of entry may be dependent on trivial differences in relationships among predictors in the sample that do not reflect population differences. Moreover, the interpretation of the variables in stepwise is not relevant. Therefore, I decided to use the direct procedure.

The results from the discriminant analysis were interpreted taking into consideration the significance of discriminant functions (chi-square tests), the plots of discriminant functions, the accuracy of the classification of cases into groups and the absolute magnitude of the standardized discriminant function coefficients' weights ('loadings') associated with each predictor (acoustic parameter). In discriminant function analysis there is no special problem with unequal sample sizes in the groups but the sample size of the smallest group should exceed the number of predictor variables. Several separate discriminant function analyses were conducted (see table 5.1.). One tested for individual differences in the context of feeding, in which only subjects for which I had 10 or more calls were selected (since the number of predictor variables was 10). A different discriminant analysis was performed between contexts (locational/feeding), testing if calls could be classified into the two groups (contexts) based on the 10 acoustic parameters. The important consideration in this analysis was that each subject's contribution to the sample in the two contexts was similar; thus, only individuals with 3-5 calls per context were selected (with a total of 44 calls per each context). Three independent discriminant function analyses, within individuals and between contexts were conducted; one for each individual for which I had a number of calls per context higher than the number of predictors to be included in the analysis (e.g. for female F1 a discriminant analysis was carried out on 26 calls, 15 given in a feeding context and 11 in a locational context, to test how accurately her calls could be classified to each context on the basis of their acoustic structure).

5.3. RESULTS

5.3.1. Descriptive analyses

Descriptive analyses were conducted for the 11 acoustic variables examined. The coefficient of variation (standard deviation of a measure expressed as a percentage of its mean; Slater 1978) is useful for comparing the extent of variability across individuals in

different features when measurements differ in magnitude (Falls 1982). Table 5.3. presents the means, standard errors and coefficients of variation for each variable in the two distinct contexts to assess the importance of each separately. In the context of feeding the parameters with highest coefficient of variation were MNF, D and MXFL (see table 5.2. for description of parameters' abbreviations). In the locational context the parameters with highest coefficient of variation were MNF, MNFL and DM.

For the analysis of the silent interval after the call both identified and unidentified subjects' calls were considered because the main interest was to discover what the average interval between *whinnies* was in the population as a whole. The average silent interval after feeding *whinnies* was 24 sec., whereas the one after locational *whinnies* was 22 sec.

A one-way ANOVA investigating the duration of the silent interval after the call in the two contexts (feeding/locational) showed that there were no significant differences between them ($F=0.22$; $p=0.640$; $df=1;164$).

To explore the statistical significance of differences among individuals and among contexts, 10 two-way ANOVAs were conducted, one for each acoustic parameter; the F-ratios and probability levels for 10 acoustic parameters are shown in table 5.4. Of the 10 parameters considered, nine showed statistically significant differences among individuals ($p<0.001$). Only the duration of the 1st modulation failed to show significant differences across individuals. None of the 10 parameters measured showed statistically significant differences between contexts (feeding/locational).

5.3.2. Discriminant analysis: acoustic variation between individuals

A direct discriminant function analysis was performed using 10 acoustic parameters as predictors of membership in eight groups. Predictors were D, #FM, D1st, DM, DL, MXF, MNF, FR, MXFL and MNFL. Groups were eight individual spider monkeys: five adult females, an adult male, a subadult female and a juvenile female. Missing data appeared to be randomly scattered throughout groups and predictors. Following Tabachnick and Fidell (1989), I estimated missing data inserting mean values, i.e. replacing the missing value with the mean of that column. Thus, 125 cases were considered in the analysis (see table 5.1).

Four significant discriminant functions were calculated, with a combined chi-square=334.5, df=70, $p<0.001$. After removal of the first function, significant discriminating ability remained for the next three functions, which had a combined chi-square=172.7, df=54, $p<0.001$. The first and second discriminant functions accounted for, respectively, 62% and 19% of the variability among individuals.

Table 5.3. Descriptive statistics on 11 acoustic parameters of whinnies given by 9 spider monkeys in the context of feeding and in a locational context

Acoustic Parameter	Mean		Standard Error		CV*		n	
	FEEDING	LOCATIONAL	FEED	LOCAT	FEED	LOCAT	FEED	LOCAT
1. (D) (sec)	1.0519	1.0293	0.097	0.038	84.4	30.1	117	67
2. (#FM)	6.32	6.14	0.214	0.331	36.2	42.8	114	63
3. (D1st) (sec)	0.087	0.093	0.002	0.003	22.9	21.5	106	60
4. (DM) (sec)	0.110	0.122	0.002	0.119	20.8	75.4	110	60
5. (DL) (sec)	0.119	0.116	0.002	0.002	20.0	14.7	103	57
6. (MXF) (kHz)	4.83	4.91	0.071	0.099	16.1	16.5	119	67
7. (MNF) (kHz)	0.25	0.42	0.033	0.108	140	207	110	65
8. (FR) (kHz)	4.61	4.59	0.059	0.098	13.4	17.2	109	65
9. (MXFL) (sec)	0.37	0.34	0.023	0.031	67.6	70.6	111	60
10. (MNFL) (sec)	0.14	0.17	0.008	0.019	57.1	82.4	98	50
11. (INTA) (sec) **	23.8	21.5	2.09	2.36	_	_	116	49

* Coefficient of variation (see text for definition)

** For this last variable both identified and unidentified monkeys' calls were considered

Table 5.4. Results of a two-way ANOVA for 10 acoustic variables.
Factor 1: subjects (9) Factor 2: contexts (2)

Acoustic Parameter	df		F-ratio		Probability	
	Factor 1	Factor 2	Factor 1	Factor 2	Factor 1	Factor 2
1. (D)	8;127	1;127	56.16	2.06	<0.001	ns
2. (#FM)	8;122	1;122	8.42	0.182	<0.001	ns
3. (D1st)	8;115	1;115	1	0.7	ns	ns
4. (DM)	8;116	1;116	3.88	0.38	<0.001	ns
5. (DL)	8;108	1;108	3.1	0.95	<0.005	ns
6. (MXF)	8;126	1;126	19.29	0.008	<0.001	ns
7. (MNF)	8;122	1;122	3.81	1.88	<0.001	ns
8. (FR)	8;121	1;121	4.40	1.78	<0.001	ns
9. (MXFL)	8;114	1;114	4.4	0.14	<0.001	ns
10. (MNFL)	8;100	1;100	61.16	0.01	<0.001	ns

A major utility of discriminant analysis is the classification of cases into groups. On the basis of the discriminant functions generated, each call was assigned to its actual group (correct individual), or to another one (incorrect individual). Of 125 calls classified, **72%** were correctly assigned to their own individual through the discriminant functions. Only 12% correct cases would be expected by chance alone. Some individuals were predicted more accurately than others (see table 5.5.). For example, of the 16 calls recorded of adult female AF DV, 15 (94%) were assigned accurately. By chance alone, 3 calls would have been cast into this category. Figure 5.4. shows a plot of group centroids (means of the discriminant scores for each individual on each function) for the two first discriminant functions, helping the evaluation of classification of cases into groups. Groups are spaced along the two discriminant functions according to their centroids. The bigger the difference between the centroid of one group and the centroid of another along a discriminant function axis, the better that function separates the two groups. The first discriminant function separated best the calls of adult female AF DV (group 5) and juvenile female Juv.F1 (group 3), while the second discriminant function distinguished best the calls of adult female AF DNB (group 4) from the ones of adult female AF DV (group 5). Some individuals were more likely to be misclassified than others (see figure 5.4., individuals with more scattered cases). Calls of individuals AF F1, AF NB and Sub.F1 (groups 1, 2 and 8) were the ones misclassified more often. For example, 4 calls (25%) of adult female AF F1 were incorrectly classified as adult female's AF NB calls (see figure 5.4.).

Discriminant analysis also provides information on which of the variables contribute most to the discrimination of individuals. The relative importance of the predictor variables (acoustic parameters) on each discriminant function was determined by examining the absolute values of the discriminant function coefficient weights associated with each variable (following Tabachnik and Fidell 1989, only those equal or higher than 0.50 were considered). The acoustic parameter contributing most to the first discriminant function (>0.50) was **MXF** of the call. All other parameters had coefficient weights lower than 0.50. The two-way ANOVA showed that the acoustic parameter MXF differed significantly between individuals (table 5.4.). As noted above, the first discriminant function distinguished best calls of an adult female (group 5) from those of a juvenile female (group 3). Calls of the juvenile female had higher maximum frequencies (mean=5.77) than those of the adult female (mean=4.0). Compared to the other subjects, these two individuals were the ones which differed most in this acoustic parameter. On the second discriminant function the variables with highest coefficients (>0.50) were **#FM** and **FR** of the call. Both showed significant inter-individual variation in the two-way ANOVA (table 5.4.).

Table 5.5. Classification of calls to individuals by discriminant function analysis

Actual Individual	Total no. calls	Predicted Individual							
		AF F1	AF NB	Juv.F1	AF DNB	AF DV	AM M1	AF UN	Sub.F1
AF F1	16	8 **50.00%**	4 25.00%				2 12.50%		2 12.50%
AF NB	33	3 9.10%	22 **66.70%**		3 9.10%	2 6.10%	1 3.00%	2 6.10%	
Juv.F1	10			8 **80.00%**					2 20.00%
AF DNB	17		2 11.80%		13 **76.50%**	1 5.90%	1 5.90%		
AF DV	16		1 6.30%			15 **93.80%**			
AM M1	12	2 16.70%					9 **75.00%**	1 8.30%	
AF UN	11	1 9.10%					1 9.10%	9 **81.80%**	
Sub.F1	10	1 10.00%		1 10%			1 10.00%	1 10.00%	6 **60.00%**

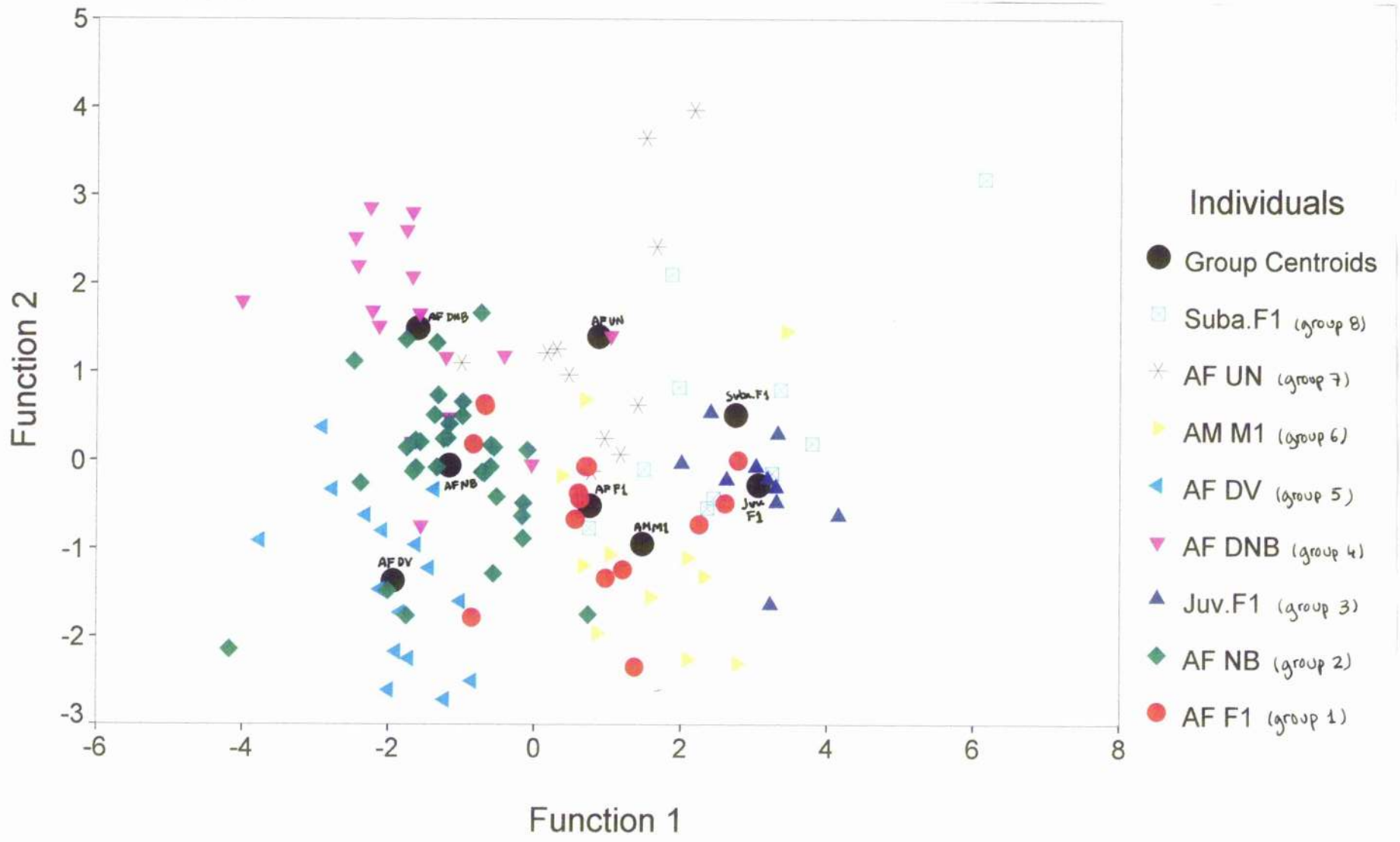


Figure 5.4. A plot of group centroids (means of the discriminant scores for each individual on each function) for the two first discriminant functions.

Thus, female AF DNB was the subject with higher number of modulations in the fundamental frequency (mean=9). Juvenile F1's calls had the largest frequency range (mean=5.19), and the biggest difference in frequency range occurred between this female and adult female AF DV (mean=3.93).

In summary, the acoustic parameter which exhibited the highest variation across individuals in both contexts, feeding and locational, was a spectral one, the minimum frequency of the call. All acoustic parameters measured, except one, duration of the first modulation, showed significant differences between individuals in the context of feeding. Thus, there were enough quantitative physical differences in the structure of spider monkey's *whinnies* to enable the discrimination of each individual's calls. Moreover, it was possible to correctly assign *whinny* exemplars to the appropriate individual, on the basis of that individual call's **maximum frequency, number of frequency modulations** and **frequency range.**

5.3.3. Discriminant analysis: acoustic variation between contexts

To test if *whinnies* given in a feeding context are acoustically different from those given in a locational one, a discriminant function analysis was conducted. *Whinnies* given in a resting context were not considered for analysis because the data sample was too small. The discriminant analysis was performed using 10 acoustic parameters as predictors of membership in two groups. Predictors entered in the analysis were D, #FM, D1st, DM, DL, MXF, MNF, FR, MXFL and MNFL (see table 5.2. for description of abbreviations). Groups were the two contexts: feeding and locational. As in the previous section, I estimated missing data inserting mean values for that column. Thus, a total of 88 *whinnies* given in the two contexts by nine subjects were included in the analysis (feeding context, n=44; locational context, n=44)(see table 5.1.).

The discriminant function calculated showed no association between groups (contexts) and predictors (chi-square=7.30, p=0.69, df=10). In the classification procedure, of 88 calls 61% were classified correctly, compared to 50% that would be correctly classified by chance alone. A total of 73% of feeding *whinnies* were correctly classified into a feeding context and 50% of locational *whinnies* were correctly classified into a locational one. After inspection of the standardized discriminant function weights, the best predictor for distinguishing between the two contexts was the call's frequency range (**FR**), with feeding *whinnies* exhibiting a greater frequency range than locational *whinnies* .

The results of the classification procedure have shown a non significant proportion of correctly classified cases (approximately 10% higher than expected by chance alone). One problem to consider in this analysis is that, since there are strong individual differences in the acoustic structure of *whinnies* (as seen in section above), it potentially confounds contextual variation with individual variation. Therefore, I decided to conduct a separate discriminant analysis for each subject (3) for which there was a call sample large enough for each context, in order to determine whether individuals retain their vocal 'signatures' across contexts.

5.3.4. Discriminant analysis: individual differences between contexts

a) Subject: Adult female AF NB

A direct discriminant function analysis was performed using 10 acoustic parameters as predictors of membership in two groups, feeding and locational contexts. Predictors were the same as in the previous analyses. A total of 48 calls from this adult female were used in the analysis, 33 given in a feeding context, 15 in a locational one. A discriminant function was calculated, showing a significant discriminating ability between contexts (chi-square=24.65, $p<0.01$, df=10). In the classification procedure, of 48 calls, 85% were classified correctly, compared to 50% that would be expected by chance alone. Both contexts had similar proportions of correctly classified cases (feeding 85% and locational 87%). The best predictors for distinguishing between contexts were duration, number of frequency modulations and minimum frequency location (see table 5.6.). The *whinnies* of this female exhibited greater duration in feeding than in locational contexts, but had more frequency modulations in locational rather than in feeding contexts. The minimum frequency of the call was located further in the call (towards the end) in *whinnies* given in locational contexts than in *whinnies* given in feeding contexts (see mean values in table 5.6.).

b) Subject: Adult female DV

For this female the size of the call sample was big enough to include *whinnies* given in the context of resting in the analysis. One acoustic variable, FR (frequency range), was not included in the analysis because it failed the tolerance test, showing evidence of multicollinearity (when variables are highly correlated). A direct discriminant function analysis was performed using 9 acoustic parameters as predictors of membership in three groups (contexts: locational, feeding and resting). A total of 35 calls were used in the analysis, 16 given in a feeding context, 9 in a locational context and 10 in a resting one. Two discriminant functions were calculated, but only the first one showed a significant discriminating ability between contexts, explaining 91% of the variability among groups

(chi-square=39.32, p<0.05, df=18). The first function most effectively separated between calls given in a feeding context from those given in a resting context. In the classification procedure, of 35 calls, 83% were classified correctly, compared to 33% that would be expected by chance alone. All calls given in resting contexts were classified in the appropriate group, while in the other two contexts, 69% of cases were correctly classified into feeding and 89% of cases were correctly classified into locational contexts. Five misclassified feeding calls (31%) were incorrectly assigned to a locational context. The three best predictors for distinguishing between contexts were maximum frequency, duration of the last modulation and number of frequency modulations. Resting *whinnies* exhibited the highest maximum frequency and number of frequency modulations, whereas feeding *whinnies* had the longest last modulation. As it was the case with the previous female, locational *whinnies* had a higher number of modulations than feeding *whinnies* (see means in table 5.6.).

c) Subject: Adult female F1

A total of 27 calls from this adult female were used in the discriminant analysis, 16 given in a feeding context, 11 in a locational one. As in the previous analysis the predictors used were the 10 acoustic parameters. The discriminant function calculated showed no association between groups (contexts) and predictors (chi-square=11.09, p=0.35, df=10). In the classification procedure, of 27 calls, 81% were classified correctly, compared to 50% that would be expected by chance alone. The best predictors for distinguishing between contexts were duration, number of frequency modulations and minimum frequency location (the same as for adult female AF NB). As with AF NB, the *whinnies* of this female exhibited more frequency modulations in locational rather than in feeding contexts. But, in contrast to AF NB her *whinnies* were of greater duration in locational rather than in feeding contexts, and the minimum frequency of the call was located further in the call in feeding whinnies than in locational ones (see table 5.6.). The high percentage of cases correctly classified achieved in the classification procedure is surprising, considering the fact that there was no association between groups and predictors (non significant chi-square). A possible explanation, suggested by Tabachnik and Fidell (1989; pp. 512), is that when sample sizes are small the results of significance testing may be misleading if there is heterogeneity of the variance-covariance matrices (as in the case with this data). 'Although in discriminant analysis inference is usually robust with respect to heterogeneity of variance-covariance matrices, classification is not. Cases tend to be overclassified into groups with greater dispersion' (Tabachnik and Fidell 1989). Thus, we have to be careful in the interpretation of these results.

Table 5.6. Summary of results of 3 discriminant analysis within subjects and between contexts

	% Cases correctly classified	Acoustic Variables discriminating between contexts	Means		
			Feeding	Locational	Resting
Subjects					
1. AF. NB	85%	**D**	1.091	1.081	_
		#FM	6.5	6.7	_
		MNFL	0.097	0.242	_
2. AF. DV	83%	**MXF**	4	4.05	4.3
		DL	0.133	0.128	0.123
		#FM	6.1	6.2	6.4
3. AF. F1	81%	**D**	0.843	1.008	_
		#FM	5.5	6.5	_
		MNFL	0.138	0.122	_

5.4. DISCUSSION

5.4.1. Summary of results

The preceding results indicate that *whinnies* of spider monkeys differed between individuals. Three frequency variables -maximum frequency, number of frequency modulations and frequency range- were the primary acoustic features that differentiated the *whinnies* of eight spider monkeys. This supports the idea that *whinnies* provide sufficient information for individual vocal recognition to take place, although playback experiments will have to be done to prove that spider monkeys also respond differently to different individuals' *whinnies*.

On the whole, *whinnies* produced in feeding contexts were not acoustically different from those produced in locational contexts. Moreover, it was not possible to correctly assign *whinny* exemplars to the appropriate context on the basis of their acoustic structure. However, this may have been due to the influence of strong individual differences present in the acoustic structure of the *whinny*. When an important contributor to acoustic variation had been controlled for, i.e. caller identity (one discriminant analysis for each of three monkeys for which enough data was collected), *whinnies* were accurately classified into feeding, locational or resting (for one individual) contexts on the basis of their acoustic structure alone. There was considerable agreement among the three adult females tested in the acoustic cues that distinguished among different types of *whinnies*. One acoustic feature that discriminated between contexts in all three monkeys was the number of frequency modulations in the call. Figure 5.5. presents a figurative graph which serves to explain these results more clearly. In this graph several *whinny* calls of three different spider monkey females are plotted against a figurative number of frequency modulations. By looking at this graph, it can be seen that one cannot draw a line that separates between spider monkey's locational versus feeding calls, but we can draw one within each monkey's feeding and locational calls. Interestingly, this same feature, i.e. the number of frequency modulations, was one of the three that discriminated better between one individual and another (see above). In all three adult females, locational *whinnies* had more frequency modulations than feeding *whinnies*. Moreover, in one adult female (AF DV), resting *whinnies* had more frequency modulations than either feeding or locational *whinnies*. The other acoustic features discriminating between females' resting, locational or feeding *whinnies* (duration, maximum fequency location, minimum frequency location) were not common to all three and varied in direction (e.g. for female AF NB feeding *whinnies* were longer than locational *whinnies*, whereas for AF F1 the opposite effect occurred, locational *whinnies* were longer than feeding ones).

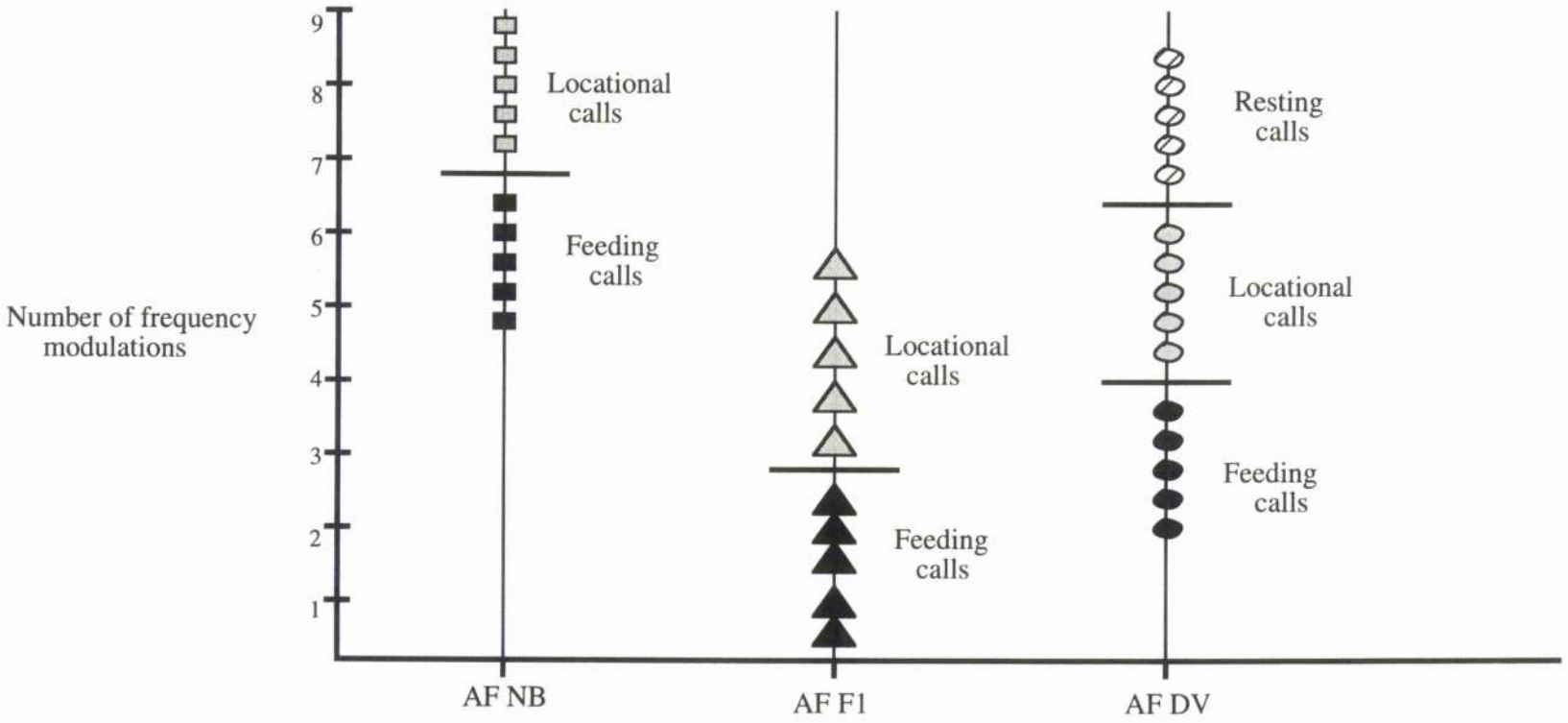


Figure 5.5. Figurative graph showing the existence of within individual variation in the number of frequency modulations of three adult females' locational, resting and feeding whinnies

Finally, these results have to be interpreted cautiously since they are based in the analysis of calls from only 3 monkeys, and the call sample for each of them was small.

Another potential limitation to bear in mind in these analyses concerns the fact of having lumped *whinnies* given in the three locational contexts: a) an individual entering a tree for the first time (fruiting or sleeping tree), b) joining a new subgroup, or c) having lost sight of the members of the subgroup with which it was travelling, into a single locational context because of scarcity of data. Although there were not quantitative behavioural differences to *whinnies* given in these 3 subcategories (see chapter 4), it does not mean that subtle acoustic differences do not exist between them or even between other categories which I have not thought of but the monkeys might be able to discriminate.

5.4.2. Potential information conveyed by the *whinny*

The results of this chapter have several implications for understanding the information that the *whinny* carries. First, the fact that locational *whinnies* were more frequency modulated than feeding *whinnies* in at least three individuals of this population, and that the number of frequency modulations was a key feature discriminating between individuals, may have important implications for the specialization of *whinnies* as localization signals. Considering that an important function of the *whinny* is to maintain contact among dispersed group members, this call might be expected to exhibit acoustic traits that facilitate the detection of conspecifics' location through a dense habitat. Apparently, clear tonal calls which exhibit frequency modulation provide better sound locatability (Waser 1977) and forest-living primates have greater frequency modulation in their call structure than ground-dwelling species (Waser 1982). However, not enough is known so far about spider monkey's perceptual abilities to draw strong conclusions on this subject.

Second, there is enough evidence to support the idea that, although spider monkeys might not use the actual acoustic features we have chosen in this study, the ability to identify conspecifics by their vocalizations alone represents a number of advantages for a species with a social organization such as the one spider monkeys have. Spider monkeys have a social structure in which a few dominant individuals have the temporal and spatial knowledge of the main food sources in the home range (Roosmalen 1980). Since individuals forage separately in subgroups of variable size and composition, the ability to choose which individuals to join could help avoiding potentially dangerous interactions with dominant individuals (Chapman and Weary 1990) or, on the contrary, could help obtaining information about the location of monkeys with the best knowledge of resources who may guide the foraging route to a highly valuable fruiting tree. Moreover, as

Chapman and Lefebvre (1990) suggested, knowing how many and which individuals are already depleting a food patch may influence the decision of whether to join a party, give food calls or, change the route of travel and forage in a different feeding site. However, a different issue concerning the ability of spider monkeys to recognize individuals by their calls is the constraint that their fission-fusion social organization may impose on such ability, i.e. it is probably more difficult for a spider monkey than for example a gorilla to remember a high number of vocal signatures from conspecifics who he/she does not encounter regularly or maintain vocal contact with for a very long time. While a gorilla spends most of its time in close contact with other conspecifics, a spider monkey may not meet the same individual twice in the same week, specially in periods of food scarcity such as the dry season.

Third, besides carrying information related to individual identity and possibly location, *whinnies* also seem to carry some information specific to the caller's situation (context). However, the acoustic features which serve to distinguish one context from another are specific to that particular individual, not common to all individuals. That is, *whinnies* per se do not provide sufficient acoustic information for listeners to discern what context the caller is in (as vervets' grunts may do), unless that listener knows who is giving the call. The acoustic structure that indicates which individual is calling seems to provide by itself the contextual information. Thus, if a male spider monkey hears a *whinny* from a female he has never heard before, he may not be able to discern if she is entering a tree full of fruit, joining a new subgroup, or has lost sight of her travelling companions. As Lillehei and Snowdon (1978) suggested, in the same way as knowledge of a situation could improve the identification of the individual calling, the identification of an individual through vocal features could provide some prediction of the situation in which the call is given. There is a possibility that certain individuals call more than others in different contexts (as Lillehei and Snowdon 1978 found in young stumptail macaques). For example, adult female NB may call more when entering fruiting trees than adult female DV because the first one is dominant over the second and has nothing to loose by attracting other individuals to the site. Unfortunately, lumping the data on the frequency of emission of *whinnies* per individual in each context to investigate this issue would not be an appropriate method since the vocal recording time per monkey was different.

5.4.3. Comparison with other studies: Chapman & Weary 1990; Masataka 1986

The results concerning the variability found in the acoustical structure of *whinnies* of different individuals confirmed what has already been discovered for the same call (Chapman and Weary 1990). However, the acoustic features of *whinnies* which best

distinguished among individuals do not exactly correspond with those found by the previous authors in the same community. On the one hand, Chapman and Weary (1990) did not find consistent individual differences in spider monkeys *whinnies'* duration of the call, number of frequency modulations or maximum frequency. On the other hand, they found that the duration of the middle and last modulations of *whinnies* were the features that best discriminated among individuals, while in my study the number of frequency modulations of the call, its maximum frequency and its frequency range were the best discriminating features. How can these divergent results (i.e. spectral features versus temporal ones) in two studies working with the same population of spider monkeys be explained? The most plausible explanation might be linked to methodological differences. Although both studies analyzed *whinnies* given in the same context of feeding, the call and individual sample used, and the statistical procedure followed was different. Chapman and Weary analyzed six acoustic features in a sample of 81 calls from 14 monkeys (range 4-10 calls per subject) using a stepwise discriminant analysis, while in my study I measured ten acoustic features (six in common with theirs) in a sample of 125 calls from 8 monkeys (range 10-33 per subject), using a direct discriminant analysis.

Masataka (1986) in a paper which has surprisingly been cited rarely in the literature (only Macedonia 1986), described a playback experiment with captive spider monkeys (*Ateles geoffroyi*) in which he broadcast *whinnies* previously responded to by individual 'A' to an audience consisting of individual 'A' plus two other individuals in close proximity. The type of *whinny* used as stimulus for the playback was one given in a context as ambiguously defined as 'an instance in which the signaller succeeds in communicating with a specific animal among presumptive signal recipients' (with no more details about what this 'successful' communication implied). He divided experimental trials into those in which he played what he called 'relevant calls' (calls originally responded to by individuals who are among the receivers of the playback), and those in which he played 'irrelevant calls' (calls originally not responded to by individuals who are among receivers). The results showed that behaviours such as giving a *whinny* or approaching the speaker were more frequent in each individual (not only in the 'original' receiver) after relevant calls than after irrelevant calls. Moreover, irrelevant animals (those that had not originally responded to the stimulus) looked at the relevant animals (those to whom the call was supposedly directed to) significantly more frequently than at another irrelevant animal. This is explained by the author by saying that monkeys could anticipate who was going to respond to a given *whinny* (something that has already been observed in vervet monkey's screams; Cheney and Seyfarth 1980). Furthermore, in a preliminary acoustic analysis of *whinnies* of different individuals he showed the existence of individually-specific differences in three (not measured in my study) out of 14 acoustic features, suggesting that these might have been used by the monkeys to make

discriminations between callers. Although he did not describe in detail the 14 acoustic parameters measured, only two of his list were common to my study. The reason for this is that the parameters he chose were mostly related to amplitude or other spectral features that need invariable recording conditions which may be achieved in captivity but not in the wild when recording highly mobile monkeys. Other important methodological difference between the two studies was that the context in which the *whinnies* in his study were given was one in which an individual or more had responded to another individual's *whinny*, regardless of whether the caller was feeding or involved in any other activity. The conclusion of the paper was that spider monkeys are able to distinguish between *whinnies* to which they originally responded to from those responded by other individuals, thus recognizing by voice alone 'who directs a *whinny* to whom'. In summary, Masataka claimed not only vocal recognition in spider monkeys, but also a representational ability of *whinnies* to function as a sort of 'names'. In my opinion the author goes too far in asserting that *whinnies* might function as names. The evidence shown in the paper is not enough to support these claims and the methods are not described thoroughly enough.

Chapter 6
Intercommunity encounters in fission-fusion primate species

6.1. INTRODUCTION

This chapter presents a theoretical review of the subject of intercommunity encounters and territoriality in fission-fusion species with the aim of setting the scene for the next experimental chapter. A fission-fusion social system was characterized by Chapman, White and Wrangham (1993) as having flexibility in both the size and composition of groups within a community. This system is exhibited by several species of primates. In the Old World: common chimpanzees (*Pan troglodytes*), pygmy chimpanzees or bonobos (*Pan paniscus*), red colobus (*Colobus badius*), hamadryas and guinea baboons (*Papio hamadryas*; *Papio papio)* and gelada baboons (*Theropithecus gelada*); in the New World, spider monkeys (*Ateles geoffroyi*), woolly spider monkeys (*Brachyteles arachnoides*) and woolly monkeys (*Lagothrix lagotricha*) show this characteristic pattern of social organization. In all of these fission-fusion species the frequency of intergroup encounters, the behaviour displayed during them and the degree of territoriality exhibited may vary depending upon several social and ecological factors which will be examined below. In a review chapter describing the characteristics of intergroup encounters among different primate species, Cheney (1986) emphasized the difficulty of making cross-species comparisons about intergroup interactions. The main reasons she gave for this were the high variability of the behaviour exhibited, the lack of data on intergroup relations and the absence of comparable measures. In the following pages I bring together the existing evidence on fission-fusion species' intergroup encounters, using a measure of territoriality which could be used for future comparisons between fission-fusion species as new data comes to surface. In the revision of the literature I use some of the information in Cheney's 1986 paper, and concentrate on the social and ecological variables which could have led individuals with similar social organization to behave differently in a comparable social situation. A table at the end of the chapter summarizing all the ecological and social variables considered will provide evidence for possible generalizations across species with a fission-fusion social system. Throughout this chapter I will use the term group as synonymous of community to avoid confusion with the terminology of other authors.

6.2. Behaviour during intergroup encounters in fission-fusion species

I will start by describing briefly the intergroup behaviour of those fission-fusion species with most similar ecological conditions, i.e. spider and woolly spider monkeys on the one hand, and chimpanzee and bonobos on the other, drawing special attention on chimpanzee/spider monkey comparisons, since a number of social similarities have been argued to exist between them (Fedigan and Baxter 1984; McFarland 1986; McFarland Symington 1990; Chapman et al. 1995). A special mention will be made of the question of territoriality in fission-fusion primate species, focussing on the possibility of spider monkeys being territorial.

6.2.1. SPIDER MONKEYS

In 1935 Carpenter described spider monkeys as semi-nomadic, with overlaping home ranges. 'Little is known of the factors that regulate the limits and the shifting of territories of different groups. It would be expected that changes in the territorial range would occur coincidently with the seasonal variations of the food supply' (Carpenter 1935). Later, five studies (Klein 1972; Klein 1974; vanRoosmalen 1980; Fedigan and Baxter 1984; Symington 1987) reported and described cases of intercommunity encounters. Klein (1972) described a few instances in which members of different large social groups of *Ateles belzebuth* encountered one another. Adult males engaged in charging, branch-shaking, growling and two type of vocalizations, *whoops* and *screams*, were frequently heard. Shortly after the encounter, embracing and pectoral sniffing among the members of the same community was seen. In a more detailed study focussing specifically on spider monkey's agonistic behaviour, Klein (1974) commented on cases of what he called 'confrontations' between different social groups in which actual physical aggression between participants (slaps, hair pulling, and even a wound injury) occurred. These confrontations ended with a deflection of travel direction or pull back by one of the groups involved. If a community consisting only of females met an all-male community, the female's reaction was prolonged 'ook-barking' as they gradually moved away. By contrast, the males' behaviour when meeting any new community was invariably reciprocal charging, sustained growling and branch-shaking. There are three particular behaviours which Klein defined as 'territorial behaviour', occurring exclusively at these intergroup confrontations: the two loud vocalizations above mentioned (whooping and

screaming), and scent-marking of tree trunks and branches, in which secretions of the external glands mixed with saliva were rubbed onto trees.

Van Roosmalen (1980) argued that only male spider monkeys (*Ateles paniscus*) are territorial and respect clearcut boundaries. Females, although usually staying within the communities' boundaries, may occasionally visit neighbouring communities for periods up to an entire day. He described the rare territorial boundary conflicts he witnessed as starting with an adult male detecting members of another community at the other side of the boundary. 'He starts uttering long calls (*whoops*) and, in cooperation with one or more females, then performs siamang-like duets which causes an invasion of subgroups to the vicinity. The members of the other group respond with similar behaviour at the other side of the boundary...' The males of both communities would shake branches, break off twigs, give *whoops* and *barks* in cooperation with females, who will show signs of excitement (pilo-erection). Behaviours such as mutual embracing and pectoral sniffing also occurred as a form of reassurance.

The main difference between Klein's (1972) and van Roosmalen's (1980) studies centres on the fact that the first one found that in La Macarena (Colombia) there was a 20% home range overlap between communities, whereas Van Roosmalen, in Suriname, did not observe any home range overlap between the study group and any of the other three communities. The geographical barriers explained why so few boundary lines between communitites existed.

In a study focussing on the social organization of spider monkeys (*Ateles geoffroyi*) at Tikal National Park (Guatemala), Fedigan and Baxter (1984) concluded that males were both more aggressive and more territorial than females. Their definition of territorial behaviour was based on the number of mobbing displays they observed during territorial confrontations taking place on each side of a road which separated the home ranges of what appeared two different communities. As in the previous studies, females, although sometimes in association with males during territorial encounters, did not actively participate in the mobbing displays. Like, Van Roosmalen (1980), Fedigan and Baxter (1984) emphasized that adult male spider monkeys cooperate in territorial defence, being thus able to defend larger territories which overlap the ranges of several females, showing a strong similarity with the chimpanzee social system.

Symington (1987) observed only four cases of agonistic interactions between different communities of *Ateles p. paniscus in* Cocha Cashu, Perú. She suggested that the size of the parties involved usually determines the outcome of the confrontation (in the four instances she witnessed, the smaller party always retreated).

During my one year study at Santa Rosa National Park (Costa Rica) I did not observe any encounter between communities. Chapman (pers. communic.), who studied the same community of spider monkeys during 6 years, followed female strangers on a few occasions into the core area of the community and never saw any interactions. He also followed females with radio collars into strangers' home ranges (5km away from their own home range); they were not attacked, just returned to their home range.

6.2.2. WOOLLY SPIDER MONKEYS

Woolly spider monkeys share with spider monkeys a closer phylogenetical origin than either species do with woolly monkeys (*Lagothrix* spp.), and are also considered to have a fission-fusion social system (Nishimura et al. 1988). However, there are a number of differences between them, mainly their diet and predation pressure. Spider monkeys are primarily frugivorous and woolly spider monkeys are thought to be the most folivorous of the Neotropical primates (Milton 1984). Woolly spider monkey do not have any potential predators (apart from humans) in their home range (with the exception of one area in the state of São Paulo, Brasil where big cats, raptors and monkeys co-exist, and one case of jaguar predation was reported; Olmos 1994). Spider monkeys are subjected to predation by wild cats and harpy eagles (see chapter 8). Despite these differences they live in a similar habitat, with similar group sizes and composition, and show very similar social behaviour patterns, marked by a fluid fission-fusion social organization. Their behaviour during intergroup encounters, the focus of this discussion, has only been described on two occasions (Young 1983; Valle et al. 1984; cited in Nishimura et al. 1988). Two different groups or communities of woolly spider monkeys, living in home ranges close to one another but not overlapping, occasionally trespassed the boundaries of their range. In these instances aggressive vocal exchange between the two groups at a home range boundary occurred but no physical contact was observed. They lasted for one and a half days, indicating intolerance towards conspecific groups, and involved primarily males. Intergroup male interactions are mainly restricted to disputes associated with the monopolization of estrous females and large food sources (Strier et al. 1993).

When comparing these two New World species, it can be seen that, although both show intolerance in intercommunity encounters, spider monkeys exhibit a higher degree of aggression. The lower level of feeding competition in woolly spider monkeys (dependent on a more predictable resource), the absence of home range overlap in the populations studied and

the fact that all of the community males mate opportunistically with a female during her receptive period, may explain the different behaviour exhibited among these two species during intercommunity encounters. There do not seem to be enough benefits for *Brachyteles* to invest more energy and time in, for example physical aggression, incurring more risk in their encounters with other communitites.

6.2.3. CHIMPANZEES

In both of the field sites in which chimpanzees have been longest studied, Gombe and Mahale (both in Tanzania), aggressive intercommunity encounters are reported in two different forms. In one form, resident males collaborate to supplant neighbours encountered during foraging. In the other, aggressive interactions occur when males patrolling borders of their own range, encounter one or more members of a neighbouring community. At Gombe, Goodall (1986) observed that when communities met there was always a strong reaction, in the form of calling, stamping feet, hooting, shaking and breaking branches. In some instances even physical contact occurred, resulting in the death of one or more individuals. When a smaller group of males met a larger group of males they retreated. If two groups of the same size met, however, the males displayed with drumming, throwing branches and gave three type of calls: *pant-hoots*, *roar pant-hoots* and *waa-barks*. These vocal challenges usually ended with one party withdrawing to its home range.

Evidence from Mahale (Nishida and Hiraiwa-Hasegawa 1985) shows that similar aggressive interactions as in Gombe between males of different communities occur, with aggressive attacks including wounds to non estrous females with infants. There are two major differences between the two sites: firstly at Mahale a large community in search of ripe fruit annually supplanted its smaller neighbour for a season; this did not occur at Gombe. Secondly at Gombe there are no well defined boundaries, whereas Nishida (1979) stated that groups at Mahale maintained their ranges with well defined 'traditional' boundaries (not ecological, but invisible barriers). Mahale males also engaged in patrolling behaviour. Nishida (1979) also commented that it was the size and composition of the parties that decided the outcome of an intergroup encounter.

Studies of chimpanzees in Guinea, Senegal, Tanzania and Uganda include drier and more open habitats. Izawa (1970) found that in Kasataki, Tanzania (savannah woodland) different communities of chimpanzees seemed to avoid one another. Even when the ranges overlapped, one group never moved into the main area of the other. The main difference in savannah and

rain forest habitats can be found in the population density and the type of environment the chimpanzees range in. Both factors seem to affect the type of interaction between different communities (Pitcairn 1974). The ranges of low density populations are too big to be defended as territories (Wrangham 1986). At Gombe and Mahale the population density is high, community ranges change slightly during the year and intercommunity interactions are frequent (Wrangham 1986). At low density, as in Senegal (Mt Assirik), where chimpanzees occupy the hottest, driest and most open habitat known for the species, the community migrates as a unit between discrete seasonal ranges (Tutin et al. 1983).

There are two main differences between intercommunity encounters in the well-studied chimpanzees along Lake Tanganyika (Tanzania) and in spider monkeys. One is the high level of physical aggression exhibited by chimpanzees, absent in spider monkeys' intergroup encounters, plus the fact that, unlike spider monkey females, whenever chimpanzee females enter the territory of a 'foreign' community they are at risk of being attacked by both resident males and females. The other difference is that the behaviour described by Goodall in chimpanzees as 'patrolling', to monitor areas outside the home range, has not been reported in spider monkeys or any other fission-fusion species. However, the possibility of encountering individuals from neighbouring communities seems to affect the grouping of spider monkeys. For example, at Cocha Cashu Symington (1987) reported that subgroups in the peripheral areas of the community range, where encounters with individuals from neighbouring communities are most likely to occur, are significantly larger than parties in the interior of the community range.

Male chimpanzees remain in their natal community whereas females, as in spider monkeys, may emigrate. Goodall (1983) and Wrangham (1986) reported cases of repeated female intergroup transfer from one community to the other at Gombe. Female chimpanzees often travel, as spider monkey females do sometimes, to the overlapping areas, near the communities' borders, but unlike spider monkeys, they do actively participate in intercommunity confrontations, directing their aggression specially to new nulliparous inmigrant females.

A few differences between chimpanzee and spider monkey mating patterns may explain the difference in the males' aggressive behaviour during intercommunity encounters. The most important difference relates to the willingness of females to be members of subgroups. Chimpanzee females exhibit large estrous swelling, often mate with a large proportion of the males in the community, are vocal during mating and change their ranging and association patterns when in estrous, to travel with males and join large subgroups. However, in spider monkeys copulations are secretive, there are no visual cues to receptivity. The second

difference is that female chimpanzees are more solitary than female spider monkeys. Spider monkey males can find females more easily than chimpanzee males: they have smaller home ranges than chimpanzees, travel a greater proportion of their range daily, and use sleeping sites with fixed locations. Thus, unlike for the spider monkey male, the benefits obtained by a male chimpanzee's aggressive behaviour in an intercommunity encounter (avoiding losing females from his own community or acquiring potential new mates) are higher than the costs of energy and injury incurred.

6.2.4. PYGMY CHIMPANZEES

Pygmy chimpanzees share the same diet, with ripe fruit as the chief energy source, with chimpanzees but, unlike them, they are exclusively restricted to continuous evergreen forests. The size of their communities are larger than those of chimpanzees and there are a number of important social differences between the two species (White and Wrangham 1988; Chapman, White and Wrangham 1994). The two field sites where they have been studied are located in Zaire: Wamba, with limited provisioning (Kano 1992); Lomako, without provisioning (Badrian and Badrian 1984). In Wamba, the home ranges of different groups or communities overlap and when two groups meet the smallest one usually avoids contact. Occasionally conflicts will emerge in the form of exchanging calls and branch dragging (Kuroda 1979) but without apparent aggression. Only one instance of an intergroup encounter, in which a fight over food leading to serious injuries to some individuals occurred, has been reported at Wamba (Kano and Mulavwa 1984). Few intercommunity encounters were observed at Lomako, where the home ranges of two communities also overlapped. Badrian and Badrian (1984) described intergroup encounters as vocal 'contests' where groups avoided each other with no physical aggression present.

When comparing the common chimpanzee with the pygmy chimpanzee we are faced with a similar case to the one of spider monkeys and woolly spider monkeys. Pygmy chimpanzees have larger and more stable party sizes than chimpanzees. Their diet, although including many fruits, is highly based in the more common terrestrial herbaceous vegetation. Thus, pygmy chimpanzees, as woolly spider monkeys, have reduced intragroup feeding competition because they use large fruit patches and consume terrestrial herbaceous vegetation. Together with this, possessive consortship matings are not known in pgymy chimpanzees and opportunistic matings in which many males participate are common. These factors may explain the fact that intercommunity encounters among pgymy chimpanzees consist mainly in

avoidance or vocal exchange without the aggressive component existing in common chimpanzees.

6.2.5. RED COLOBUS

Of all colobines studied, the red colobus seems to be the only one that exhibits a fission-fusion social system. In Kibale forest there is complete home range overlap among social groups (Struhsaker 1975). During intergroup encounters vocal exchanges occur between males of different groups, mainly *chists*, *wheets* and *barks,* which may be heard at distances up to 300m. The outcome of interactions is extremely variable. Groups may avoid one another, be tolerant of each other, or males may exchange vocalizations, branch-shake, perform 'leaping-about' displays and chase one another (the maximum level of aggression being spatial supplantations of one group by the other). The most aggressive incidents involve exclusively adult, subadult and juvenile males. During these intergroup conflicts the males show an exceptional degree of cohesion and unity against the other group. However, males do not show resource defence. Thus, it is believed that these males' coalitions defend females as reproductive resources against other male coalitions, as occurs in chimpanzees. Struhsaker (1975) concluded that, since there is extensive overlap in home range and frequent tolerance of other group's proximity, the red colobus do not seem a territorial species. Clutton-Brock's (1974) observations of intergroup encounters at Gombe are similar to Struhsaker's. However, Marsh (1979) who studied red colobus in a different habitat, i.e. gallery forests along the Tana River, Kenya found little home range overlap in groups of a smaller size than those studied by the previous authors. Half of the intergroup encounters he observed were clearly aggressive (displays and vocalizations), whereas in the other half no aggression was displayed.

In conclusion, chimpanzee and red colobus males, like spider monkey males, form cooperative alliances against males from other groups. However, unlike spider monkey males, chimpanzee and colobus males exhibit high levels of within group male-male agonism.

6.2.6. HAMADRYAS, GUINEA AND GELADA BABOONS

Although not mentioned as often as typical fission-fusion species, hamadryas, guinea and gelada baboons do typically form small units which forage independently and are part of a

larger group. The main difference is that the fission-fusion of the baboons' band (chimpanzees' community) into clans (as defined by Stammbach 1986) is restricted to a foraging context, whereas in all of the species mentioned above fissioning occurred at all levels and sometimes a subgroup will range separated from the rest of the community for two consecutive days or even months. Thus, in baboons, subgroup size and composition are rather rigidly structured in contrast to the other fission-fusion species. Moreover, their diet, habitat and social organization differs from the species reviewed above. The risk of predation is high for all baboons.

In hamadryas, adult baboons seem to avoid interband encounters, and few cases of physical aggression between males of different clans have been described. The females always have a passive role in these instances. In the case of geladas, which have an extensive overlap in ranging areas, bands seem to be more tolerant of other bands, accepting them and even merging into large mixed bands. According to Dunbar (1984), since grass is a uniformly distributed resource, gelada baboons do not defend territories and have long day journeys compared to the small size of their home ranges. Guinea baboons in Senegal form very large groups which disperse repeatedly into small unstable parties (Dunbar and Nathan 1972; Byrne 1981). The two factors that seem to cause troop fission are poor visibility and a local limit to the number of suitable sleeping sites (Dunbar and Nathan 1972). Byrne (1981) found that Guinea baboons in Senegal used two types of loud calls (barks) in intergroup coordination, specially when a large group was fissioning into subgroups during feeding, as a way of maintaining contact with each other through the dense bush and facilitating the reunion of the troop before crossing any open area.

The reason for the lack of territorial and aggressive behaviour during these encounters may be that the resources are abundant and scattered enough, so there is no intergroup feeding competition. Moreover, there is no female interband transfer.

6.3. Territoriality in fission-fusion species

The fission-fusion species reviewed above seem to show different degrees of aggressiveness and intolerance towards neighbours during intergroup encounters. A species considered territorial would exhibit a particular behaviour when encountering neighbours or strangers in its home range who represent potential competitors for food and mates. But, when can we call a species territorial? Maher and Lott (1995) published a detailed review of the literature on territoriality, concentrating on the definitions of the term given by animal

behaviourists to date. They found that the most common definition of a territory is a 'defended space'. Thus, a species could be called territorial if it defended an area to exclude other animals. The three criteria most commonly used in the definitions were: 'defended area', 'exclusive area' and 'site-specific dominance'. Most primate researchers used one or other of these three criteria in their definition. Maher and Lott (1995) proposed a conceptual definition of territory, which I will use from now onwards in order to discuss the degree of territoriality exhibited by the fission-fusion species reviewed above. According to these authors a territory is 'a fixed space from which an individual, or group of mutually tolerant individuals, actively excludes competitors for a specific resource or resources'. To operationalize this definition the authors suggested to determine the degree of home range overlap. A different way of operationalizing this definition can be found in Mitani and Rodman's paper (1979), in which they focussed on territory as defended area and introduced an index of defendability to examine the distribution of territoriality among primate populations. Their index was based on the ratio of mean day journey length to the diameter of the territory.

I used the index of defendability suggested by Mitani and Rodman (1979) to compare the ability of the different fission-fusion species to monitor the boundaries of their ranges (see table 6.1.). A high value of 'D' (index of defendability) implies that the species has frequent contacts with its range boundaries, thus its range is defendable. A small value indicates that defence is difficult since the range is too big to cover distant points daily. Species with ratios of less than one were usually non-territorial in their study.

Within the different field sites where the genus *Ateles* have been studied, all populations have a high value of D (D>1), suggesting that spider monkeys have enough mobility around their range for maintaining a territory. This is also the case for woolly spider monkeys. Of the other fission-fusion species, only hamadryas and guinea baboons have a high index. Both chimpanzees and pygmy chimpanzees, gelada baboons and red colobus have a low defendability index (D<1) which suggests that these species may have problems defending their territories since they may not be able to afford visiting the boundaries of their range frequently enough.

However, there are four cases in the table that are difficult to explain. In the first place, according to Mitani and Rodman (1979), species with day journey lengths shorter than the diameter of the territory (see chimpanzees and pygmy chimpanzees in table) should be unable to defend territories. We have seen in the previous section that common chimpanzees specially, and pygmy chimpanzees to a lesser extent, are species which do behave territorially, patrolling and defending an area where resources and potential mates are found.

Table 6.1. TERRITORIALITY IN FISSION-FUSION SPECIES

* Mitani & Rodman's 1979 index of defendability (D)

Species	Home range area(km2)	Day range (km)	(D)*	Territorial?	Reference
Ateles paniscus (Suriname)	2.2	5	2.99	Yes	van Roosmalen 1980
Ateles belzebuth (La Macarena, Colombia)	3.9	4	1.79	Yes	Klein & Klein 1976
Ateles geoffroyi (BCI, Panama)	1.15	3	2.48	Yes	Richard 1970, Dare 1974
Ateles geoffroyi (Tikal, Guatemala)	5	?	?	Yes	Cant 1978
Ateles paniscus (Manu, Peru)	1.92	1.9	1.22	Yes	Symington 1987
Ateles geoffroyi (Santa Rosa, Costa Rica)	0.624	3	3.37	Yes	Fedigan et al. 1988
Brachyteles arachnoides	1.5	1.6	1.15	Yes	Young 1983
Pan troglodytes	13	3.9	0.95	Yes	Wrangham 1979,1986
Pan paniscus	22	2.4	0.45	Yes	Wrangham 1979,1986
Colobus badius	0.353	0.6489	0.97	No	Struhsaker 1975
Theropithecus gelada	1.9	1.26	0.8	No	Iwamoto & Dunbar 1983
Papio hamadryas	21.5	9.4	1.79	No	Dunbar 1988
Guinea baboon	29	7.9	1.29	No	Dunbar 1988

Furthermore, two species which have large defendability indexes, hamadryas and guinea baboons, do not in fact defend territories. In this respect, Lowen and Dunbar's paper (1994) is useful. They re-examine the Mitani-Rodman index and propose an alternative defendability index. Their new index ('M') not only discriminates more precisely between territorial and non-territorial species, but can also be applied to species that live in dispersed groups, as is the case of chimpanzees. In connection to boundary collision rates from the kinetic theory of gases, their index adds crucial new elements to the older one: the length of the boundary, the frequency of collisions with the boundary of the territory and the mean number of independently moving foraging parties in the home range. Thus, they argue that defendability is a function of both the frequency of boundary collisions and the length of the boundary that has to be monitored. When this index is applied to 10 populations of *Papio*, the value for guinea baboons is much lower than the discrimination point which best distinguishes between territorial and non-territorial species, consistent with the finding that this species does not defend territories. There are no data for hamadryas baboons. For chimpanzees the new index confirms the behaviour observed in the field, that they are a territorial species (although it was listed as non-territorial by Mitani and Rodman 1979). The most important advantage of the Lowen and Dunbar's index is that it allows consideration of situations in which either the detection distance or the number of independently foraging parties varies under different habitat conditions. However, they do not apply their new index to spider monkeys, another species that live in dispersed groups, or red colobus.

In summary, the fission-fusion species that can be described as territorial, according to the criterion of territory as defended space, are: spider monkeys, woolly spider monkeys, chimpanzees and pygmy chimpanzees. However, in relation to the definition of Maher and Lott (1995) there is a last aspect that I want to point out. If we remember the definition of territory given by these authors, it included a 'fixed space' in which competition for a 'specific resource' would take place. The defendability of resources can depend on the resource quality and distribution in time and space (Davies and Houston 1978). In the case of spider monkeys and chimpanzees, their spatial utilization patterns is restricted by resources (fruits) which are highly unevenly distributed and seasonal. The maintenance of a fixed home range is probably arduous for animals which feed on these type of resources, concentrated in space and intermittent in time. Thus, at least in the case of spider monkeys, my observations in Santa Rosa lead me to think that their territorial behaviour may not be limited to an exclusive large space but to small, rotatory core areas in which fruiting of important trees for their diet occur.

6.4. DISCUSSION

6.4.1. Comparison of fission-fusion species' intergroup behaviour

The reaction of the different fission-fusion species reviewed, when finding intruders from another commmunity in their range (see summary table 6.2.), show several similarities. In almost all species it is mainly males who take the active role, cooperating with each other in territorial defence. Chimpanzee and spider monkey males show a high degree of cooperation in territorial defence, being able to defend large territories which overlap the ranges of several females. However, female chimpanzees, in contrast to spider monkey females, participate actively in the conflict, exhibiting aggressive behaviour towards nulliparous immigrant females. The level of physical aggression in these encounters can be seen as a continuum from avoidance of other groups (hamadryas baboons) in one end, to wound injuries and even death (chimpanzees) in the other end. In spider monkeys it reaches a middle grade, limited to mobbing and exceptionally a wound injury. In woolly spider monkeys, pygmy chimpanzees and red colobus the level of violence is low, limited to vocal exchange and sometimes avoidance. In the baboons is almost non-existent, with a particularly high degree of tolerance in geladas.

There are a number of social and ecological factors that influence each of this species' intergroup behaviour (see table 6.2.), but the particular factors that drive males to behave aggressively and compete with other males during intercommunity encounters seem to be similar in the four species (chimpanzees, spider monkeys, woolly spider monkeys and red colobus), i.e. mainly the access to females as reproductive resources and the monopolization of large food sources. Moreover, in pygmy chimpanzees, intercommunity encounters seem to facilitate the transfer of females between communities.

6.4.2. Territoriality

We have seen that it is possible to use a measure, i.e. the defendability index, to make comparisons between different fission-fusion species, on the basis of these species' home range size, and daily range. Thus, we were able to predict which species could potentially monitor the boundaries of its range and act territorialy.

Table 6.2. Summary. Social and ecological factors possibly affecting intergroup encounters in fission-fusion species

Species	Type of habitat	Home range km2	Daily range km	Home range overlap	Diet & dispersion of resources	Group size (mean)	Population density (e)	Intergroup transfer	Intergroup Calling	Territoriality index D or M (a)	Behaviour at intergroup encounters	References
Spider monkeys	Evergreen and semideciduous forests	2.46	3.75	Yes & No	Frugivorous Highly disperse	30	7.2	Female	Yes (whoops, screams, growls ook-barks)	D=2.37 (mean of different field sites)	Physical aggression by males	van Roosmalen & Klein 1988
Woolly spider monkeys	Evergreen and semideciduous forests	1.5	1.6	No	Folivorous Low dispersion	28	17.8	Female	Yes (barks)	D=1.15 M=0.21	Aggressive vocal exchange, mainly males No physical aggression	Nishimura et al. 1988 Fonseca 1994
Chimpanzees	Evergreen forest Savannah woodland	5-300	3.9	Yes	Frugivorous and meat Highly disperse	52 (d)	3.1	Female	Yes (pant-hoots, roars, waa-barks)	D=0.95 M=0.012	High levels of Physical aggression by males & females	Wrangham 1986
Pygmy chimpanzees	Continuous evergreen forests	22-60	2.4	Yes	Frugivorous and meat	80	2.3	Female	Yes	D=0.45	Avoidance Vocal exchange	Wrangham 1986
Red Colobus	Evergreen forests and gallery forests	.35-.71	0.65	Yes	Folivorous Highly disperse unripe fruit	34	300	Female	Yes (chists, wheets and barks)	D=0.97	Vocal exchange and supplants by males	Marsh 1979 Struhsaker 1975
Hamdryas baboons	Dessert steppe	21	10	Yes	Frugivorous and omnivore	68 (b)	3.2	Male (c)	?	D=1.79	Avoidance	Kummer 1968 Dunbar 1988
Gelada baboons	Montane grassland	1.9	1.26	Yes	Graminivore	144	76.2	Male	?	D=0.81 M=0.026	Tolerance and merging of bands	Dunbar 1984 Dunbar 1988
Guinea baboons	Woodland savannah	29	7.9	Yes	Frugivorous and omnivore	184	6.3	?	Loud calls for intergroup coordination	D=1.29 M=0.007	No range defense	Dunbar & Nathan 1972 Byrne 1981 Dunbar 1988

(a) D= Mitani & Rodman's 1979 defendability index. M=Lowen and Dunbar's 1994 new index. Not calculated for some species.

(b) In hamadryas and gelada the group size given corresponds to the band size, (equivalent to the community size in spider monkeys, chimpanzees, pygmy chimpanzees and woolly spider monkeys)

(c) Female dispersion at the level of the unit. Male dispersion at the level of the clan.

(d) Average of values given for different field sites (Wrangham 1986).

(e) Number of individuals per square kilometer.

After using a second index which added several new variables to the model, e.g. the number of foraging independent parties, most of the predictions coincide with the behaviour observed in these species.

However, the classical description of territoriality includes the following points:

- conspecifics from neighbouring social groups who intrude into the home range are aggressively expelled
- boundaries are visited frequently and monitored
- auditory displays may be exchanged between adult males from different communities, as ritualized aggressive displays
- boundaries may be respected over a number of years.

According to this, only chimpanzees adhere strictly to a classical description of a territorial species. Goodall (1986) concluded that chimpanzees are territorial but theirs is a form of territoriality that has change from the ritualized, peaceful maintenance of a territory towards a more aggressive type of behaviour (with injures, elimination of intruders, recruitment of new partners, etc.). Thus, the costs of having a territory will be high for the chimpanzee (time and energy spent in patrolling borders, displaying and chasing of intruders, danger of injury or death), whereas the spider monkey does not seem to invest this amount of energy and risk.

The home range of spider monkeys at Santa Rosa is 62.4 hectares in an habitat of semideciduous forest in which some isolated patches of evergreen forest exist. The fact that neither I (in 12 months) or Chapman (in 6 years; pers. communic.) observed any intercommunity encounter makes it difficult to draw any conclusion about this population's territorial behaviour. A possible explanation for this absence of intergroup confrontations may be the same as the one explaining why territorial boundary conflicts were so rare in Suriname, i.e. that there are few boundary lines existing within the home range of the study group, caused by the isolation of the semidecidous forest they inhabit, with barriers consisting of pastures and farmland (in the case of Suriname the few boundaries were caused by geographical barriers).

In an attempt to provide some information about spider monkeys' territorial behaviour, I present in the next chapter playback experiments in which an intruder's call from a different community was broadcast in the Santa Rosa community's home range .

Chapter 7*
A test for vocal discrimination of familiar individuals versus strangers' vocalizations

7.1. INTRODUCTION

We have seen in the previous chapter that all species of the genus *Ateles* can be considered territorial. Five studies reported instances of intercommunity encounters in which varying degrees of aggression were exhibited (Klein 1972; Klein 1974; vanRoosmalen 1980; Fedigan and Baxter 1984; Symington 1987). Moreover, most species used loud calls for intercommunity spacing.

In a fission-fusion species such as the spider monkey, a frugivorous forest-living primate, it is adaptive for an individual to be capable of locating or distinguishing members of a different community from those of its own social group. There are several ways a spider monkey can do this, i.e. using visual, olfactory or vocal cues to distinguish intruders from members of its own group. Olfactory marks, though present in the spider monkey communication system, do not seem to function in long range communication but most often in sexual contexts. The limitations of visibility in tropical forests make visual information less effective than vocalization for long distance identification. Therefore, vocal discrimination is likely to be a more effective means of determining whether the conspecific is familiar or not. Moreover, there may be a number of benefits of being able to locate or distinguish, by vocalization alone, members of a different community from those of its own. Strangers are potential competitors for food and reproductive partners, and it would generally pay an individual to avoid them; additionally, if the outcome of an aggressive intercommunity encounter depends on subgroup size (as it was suggested by Symington 1987), it would thus pay an individual to be able to estimate a stranger's subgroup size before close contact is risked. But can spider monkeys in fact make such discriminations? This study describes an experimental investigation of this question, using field playback.

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The experimental playback technique has proved successful in investigating whether primates respond differently to calls from familiar individuals compared with calls from strangers or intruders. In Chapter 5, I mentioned a few examples of studies which showed evidence of individual vocal recognition of familiar individual calls. Individual vocal recognition of familiar individuals versus strangers' calls has also been documented in several primate species (cotton-top tamarins: Snowdon et al. 1983; mantled howling monkeys: Whitehead 1989; grey-cheeked mangabeys: Waser 1977; gibbons: Mitani 1985a). For example, Waser (1977) demonstrated that the 'whoop-gobble' of the gray-cheeked mangabey (*Cercocebus albigena*) mediated intergroup avoidance and that mangabeys were able to distinguish their own loud calls from neighbouring ones, responding differently to them. Whitehead (1989) found that mantled howling monkeys (*Alouatta palliata*) responded in a site-dependent way to experimental playback of loud vocalizations (roars). Howling monkeys adjusted their responses to simulated intruders depending on the quality of local patches of forest. Similarly, Snowdon et al. (1983) found that cotton-top tamarins (*Saguinus oedipus*) have individual-specific differences in the structure of their 'long-calls' and could discriminate between the long calls of familiar versus unfamiliar individuals.

Chapman and Weary (1990), and this thesis (see Chapter 5) found that in one particular vocalization of the spider monkey (*Ateles geoffroyi frontatus*) acoustic differences existed between the calls of different individuals, consistent enough in principle to allow individual vocal recognition. This call is the *whinny*, described as a 'positional indicator that accompanies feeding' (Eisenberg 1976), but may be given in a variety of other contexts (see Chapter 4).

The focus of the experiments presented in this chapter is to find out whether spider monkeys can use the information present in *whinny* calls to discriminate between strangers and familiar individuals by their calls alone. This question has clear implications for an understanding of the nature of intercommunity interactions and spacing of communities in this fission-fusion species. In relation to this an additional question that will be discussed is that, if spider monkeys are able to distinguish an intruder's call from that of an individual of its own community, are acoustic cues enough to elicit a territorial response in this species?

7.2. METHODS

The design of the experiment and the protocol followed was basically identical to the one described in the playbacks of Chapter 4 (section 4.2.). I describe in the following paragraphs the relevant information, a few details that differed and potential execution errors when conducting playback experiments.

Study site and subjects

Playback experiments were conducted in Santa Rosa National Park. The community on which experiments were performed, the 'Santa Rosa' community, consisted of about 60 individuals, fragmenting daily into subgroups of variable sizes. Because of this fission-fusion social system the experiments had to be carried out in a completely opportunistic basis.

Selection and preparation of acoustic material

The *whinny* calls used were taped-recorded from identified individuals during spontaneous bouts of calling, always in the context of feeding. The reason why the *whinny* was chosen is that it is a medium-range call (see acoustical description in Chapter 5), which occurs frequently and does not provoke a dramatic response in the receivers when heard from familiar individuals, as some other calls in the spider monkeys' repertoire do (e.g. the alarm *bark*). As in Chapter 4, the best quality calls and those with minimum background noise were selected; however, some had to be filtered (4 out of 11 samples) to reduce background noise.

Two types of trials were conducted, experimental and control trials. In the experimental trials, *whinny* calls given by monkeys from the 'Playa Nancite' community (17km from study area) were used as 'stranger' calls. This community was formed in 1987 and has never been in contact with the Santa Rosa community. In the control trials, *whinny* calls of monkeys from the Santa Rosa community were used as 'familiar' calls (same feeding *whinnies* as the ones used in Chapter 4). Two tapes were prepared, one consisting of *whinnies* originally given by individuals within the Santa Rosa community ('familiar' callers), and the other with *whinnies* given by individuals from Playa Nancite community ('stranger' callers)(see table 7.1.).

Table 7.1. Number of trials conducted with each whinny sample in the two types of playback

Type of playback	Individual	Number of trials conducted
EXPERIMENTAL	A.F. WHINNY-A	5
"strangers' calls"	A.F. WHINNY-B	4
Nancite	A.F. WHINNY-C	1
Community	A.M. WHINNY-D	2
	Juv.F.WHINNY	1
	A.F. DNB. WHINNY	3
CONTROL	A.F. F1. WHINNY	2
"familiar callers' calls"	A.F. NB. WHINNY	2
Santa Rosa	A.M. M1. WHINNY	1
Community	Juv.F.WHINNY	1
	Sub.F.WHINNY	1

Protocol

Playback trials were conducted from September to November 1994 (wet season). In total, 23 trials were conducted, 13 experimental and 10 control ones. All details about equipment used and procedure followed during the playbacks can be found in chapter 4 (section 4.2.1.).

Most trials were conducted either in the early morning between 5.00 and 6.30am while the animals were still resting in a sleeping site (n=3), or in the late afternoon.

Half the control trials were carried out in the morning and half in the afternoon. Of the 13 experimental trials, eight were conducted in the morning and five in the afternoon.

Two conditions had to be met before a trial began: (a) when a playback of a call from an individual of the same community was to be conducted, the caller itself was not among the audience; (b) no two trials were ever conducted on the same individuals on the same day. The order of playback trials of familiar or stranger callers was randomized. The design of the experiment is described in Chapter 4, figure 4.4.

In five of the 23 trials only the first two playbacks of the call were made because the subgroup began to leave the site, some individuals approached too close to the speaker, or a sudden gust of wind started. (Since these 'two-call trials' occurred on four experimental trials and only one control trial, any distortions of the data would have been against the hypothesis of discriminability.)

Data collected during trials

The information collected in each trial consisted of the recordings of all the calls given in response to the playbacks and a descriptive narration spoken into a tape recorder and transcribed into a written report each evening. In each trial the data recorded included the same information as the one recorded in the playbacks of Chapter 4 (general, receivers' information and responses to the playbacks). Only some of the behavioural categories scored were different.

Behavioural categories were selected for scoring on the basis of previous observations of responses to spontaneous use of these calls, and of territorial behaviour described in the literature. If several individuals were visible, the behavioural response of the majority was recorded; if there were only two receivers the behaviour of the monkey who was more visible was scored.

* **Look** in the speaker's direction: an individual changes the position of its head, orienting it towards the speaker.

* **Scan**: an individual is in an alert position, lifting its head up but not looking in the direction of the speaker.
* **Approach** the speaker: locomote towards the speaker.
* **Move away**: an individual locomotes away from the speaker location without a rushing movement.
* **Flee** from playback site: an individual rushes away, abandoning completely the playback site.
* **Give *whinny*.**
* **Give other type of call** (alarm *barks*, *squeals*)
* **Congregate**: whenever an individual who was dispersed comes closer to others in the same tree.
* **Mob**: mobbing was defined by Klein (1972) and Fedigan and Baxter (1984) as a 'territorial display', including several individuals leaping, branch shaking, scent-marking tree trunks and branches, mutually embracing, mounting each other and giving vocalizations, such as growling, whooping and barking.
* **Branch shake**: an individual moves branches vigorously. Scored as an isolated behaviour when occurs independently of all other behaviours present in mobbing (above).

The latency to respond was measured from the first time the call was played. Although the data analyzed only included responses occurring during the 10 minutes after the last time the call was played, the monkeys' behaviour was recorded for an hour.

Potential execution errors in playback experiments

Following McGregor et al. (1992) I mention here some of the features affecting execution errors in playback experiments and how they were minimised in this study. In relation to the test sounds used, I filtered and edited (Sound Edit Pro) some of the signals in order to remove background noise. Since most trials were conducted during the wet season, the weather conditions were fairly constant for all of them, e.g. wind was not as strong as in the dry season. In relation to the procedure and playback equipment, the speaker directionality and the position of observers were held constant during all trials.

Most playbacks were conducted with habituated individuals who could not have reacted to the playback because they associated the sound with the observers. The monkeys were already used to seeing us following them with and without a playback being conducted. We never made a playback trial immediately after finding the monkeys but waited some time, so we would not confuse their response to the playback with their first reaction to observers.

In order to show that there was no habituation of the monkeys to the playback procedure I have drawn a graph of the total number of calls given in each of the 33 trials conducted (presented in both Chapter 4 and this chapter)(see figure 7.1.). The response (total number of calls) of the monkeys to the playbacks did not seem to decrease in the latest trials.

7.3. RESULTS

The target subgroups in my playbacks varied in size, although this difference was not statistically significant (t=1.80; p=0.08; df=18). I therefore need first to establish whether subgroup size influenced the probability of an individual's vocal response. Note that, since the probability of a call eliciting a response in the audience depends on the number of individuals which can potentially respond, the raw frequencies would be misleading. These raw data were therefore divided by the number of individuals present who could potentially respond, and these data were used in tests. In order to investigate the effect of the hearer's subgroup size on the vocal responses, target subgroups were divided into three categories: small (1-3 individuals); medium (4-5); large (more than 5) (table 7.2.). In playbacks of familiar callers' *whinnies*, the only trials in which calling occurred were when a small subgroup was receiving the call, so no test could be applied. In playbacks of strangers' calls, the subgroup size had no significant effect on the number of individuals responding (H=1.10, p=0.57, df=2; Kruskall-Wallis test, adjusted for ties), the number of calls given per individual (H=1.39, p=0.49, df=2) or on the latency to respond (H=1.86; p=0.39; df=2). A Chi-square test was performed on the responses *give whinny* and *scan*. The subgroup size had no significant effect in these (*give whinny:* Chi-square=4.76; p>0.05; df=2; *scan:* Chi-square=2.98; p>0.2; df=2).

I therefore conclude that the probability of a vocal reaction, other things equal, will increase linearly with the number of monkeys in the subgroup. Thus 'calls per individuals' is the appropriate measure for subsequent analyses. Using this measure, the actual number of calls given per individual in playbacks of familiar versus strangers' calls did not differ (Mann-Whitney, W=177; p=0.18). Spider monkeys appear not to discriminate between the two sorts of playback.

However, some features of the results question this simple conclusion. Only 3 out of 10 trials in which familiar callers' *whinnies* were played elicited any vocal response, compared with 11 out of 13 stranger trials (Fisher Exact Probability test, p=0.025). This result is robust. I removed from the analysis three trials in stranger calls' playbacks with the largest subgroups, and two trials in familiar calls' playbacks with the smallest subgroups, the mean

subroup size becomes essentially the same (mean strangers'=4.4; mean familiar=4.3). Nevertheless, with this reduced data set a Fisher Exact test still revealed a significantly larger number of strange callers' trials than familiar callers' trials eliciting a vocal response (Fisher Exact test, p=0.02).

Furthermore, the only instances of *flee*, *mob*, *congregate*, *move away*, *branch shake* and *give other type of calls* (alarm barks, squeals) occurred when the call played back was from another community (table 7.3.).

It was mostly the males who started what seemed a defensive reaction, joined by the females a little later. These behaviours were admittedly recorded on only two trials (out of the 13 in which a stranger call was played back), and in both of them the subgroup size was large: 15 and 11 individuals. Thus they may reflect a qualitative shift in response for individuals in the largest subgroups; note, however, that I found no effect of subgroup size on an individual's frequence of response, in general. In other ways the responses to the two types of call were similar. Behaviours noted in playbacks of both stranger and familiar calls - *look* towards speaker, *give whinny, approach, scan* - did not occur in more trials of one type rather than the other (Fisher Exact Probability test, p= 0.28, 0.11, 0.44 and 0.38, respectively; see table 7.3.). There were no significant differences in the latency to give a call after the two types of playback (W=77; p=0.42; adjusted for ties, see table 7.2.).

As I did in Chapter 4, in the following analyses I examine the effects of various independent variables on monkeys' reactions to playbacks, plus the effect of a new one, not examined in that chapter, i.e. sex of the caller. I analyze systematically the latency to respond and the frequency of vocalizing, but other responses were often given too infrequently for statistical treatment. I present below all cases that could be tested.

The arousal level of a monkey hearing a stranger's call might affect its responsiveness; thus the monkeys' activity while hearing the playback might influence their response. Again, no such effect was found, either on the amount of calling or on the latency to respond. Kruskall-Wallis tests, adjusted for ties, were performed on the number of calls given per individual, and on the latency to respond, in the three different activities, moving, resting and eating. No significant difference emerged with strangers' playbacks (number of calls per individual, H=0.68; p=0.71; df=2; latency H=2.55; p=0.28; df=2, see table 7.2.). The data set was too small to test the results for the playbacks of familiar callers.

Activity varies during the course of the day, and this also might affect responsiveness: time of day effects (morning or afternoon) were therefore examined. When the data were sufficient to permit statistical analyses, there were no significant effects.

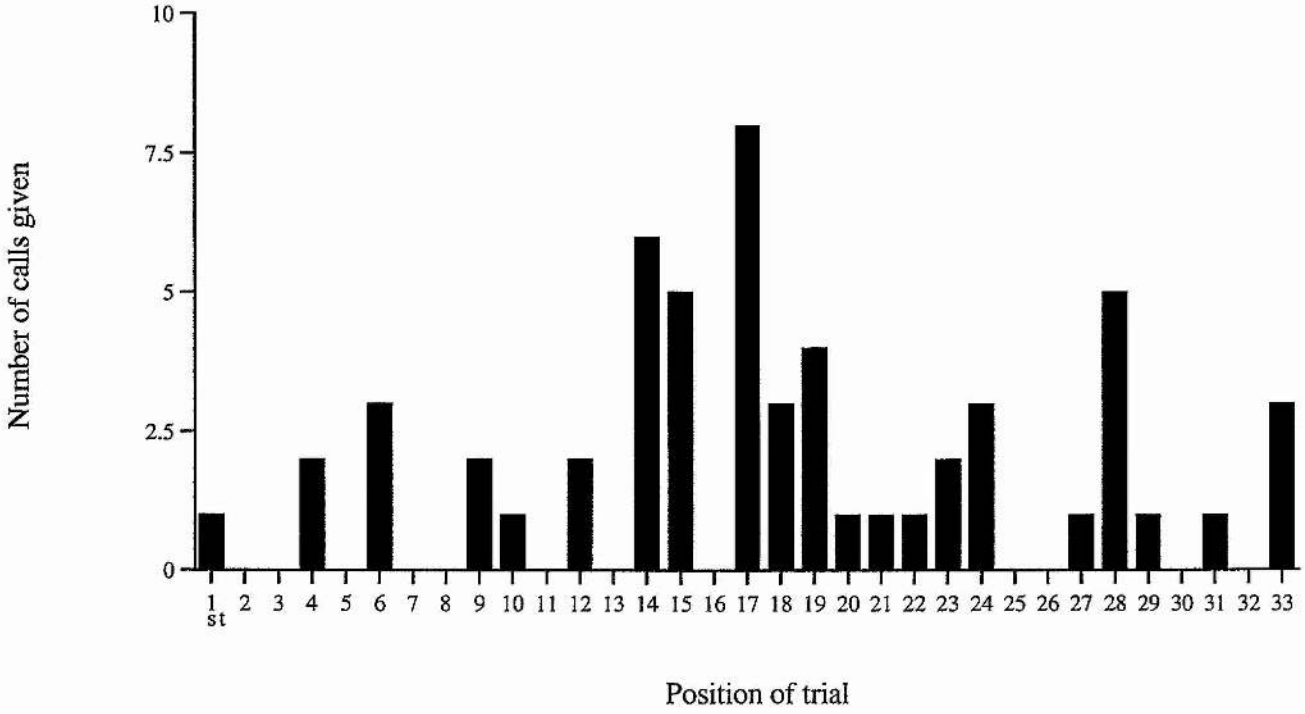

Figure 7.1. Total number of calls in each playback trial

Table 7.2. Effect of subgroup size, activity, location, sex of the caller and time of day on calling behaviour

TOTAL TRIALS: 23

	TRIAL #	DATE	TIME DAY	SLEEP SITE	SEX CALLER	SUBGROUP SIZE	ACTIVITY	TOTAL CALLS	N.INDIV RESP.	LATENCY
STRANGERS' WHINNIES	1	7/9/94	afternoon	N	M	2	moving	1	1	5sec
	2	15/9/94	afternoon	N	F	5	eating	3	3	4sec
	3	20/9/94	morning	Y	F	3	resting	0	0	_
	4	22/9/94	afternoon	N	F	2	moving	0	0	_
	5	28/9/94	morning	N	F	4	eating	1	1	3 sec
	6	4/10/94	morning	Y	F	4	moving	2	2	7sec
	7	7/10/94	morning	N	F	15	eating	>4	4	2sec
	8	11/10/94	morning	N	F	11	eating	>4	4	3sec
	9	27/10/94	morning	Y	F	3	resting	1	1	3sec
	10	28/10/94	afternoon	N	M	8	eating	1	1	2sec
	11	28/10/94	afternoon	N	F	8	eating	2	2	12sec
	12	29/10/94	morning	N	F	15	eating	3	3	3sec
	13	9/11/94	morning	N	M	5	eating	1	1	5sec
FAMILIAR CALLERS' WHINNIES	1	13/9/94	morning	N	F	3	resting	0	0	_
	2	30/9/94	morning	N	F	3	eating	0	0	_
	3	4/10/94	morning	N	F	10	eating	0	0	_
	4	19/10/94	afternoon	N	F	3	resting	3	2	3sec
	5	19/10/94	afternoon	N	F	3	eating	4	2	5sec
	6	8/11/94	morning	Y	F	4	resting	0	0	_
	7	15/11/94	afternoon	N	F	2	resting	0	0	_
	8	18/11/94	afternoon	N	F	2	resting	1	1	8sec
	9	18/11/94	afternoon	N	F	5	moving	0	0	_
	10	21/11/94	morning	N	M	4	moving	0	0	_

Table 7.3. Number of trials in which different responses were given to whinnies of different origins

	Look speaker	Scan	Approach	Give whinny	Flee	Mob	Congregate	Branch shake	Move away	Give other calls
Strangers' whinnies (13 trials)	11	10	2	8	3	1	2	1	6	3
Familiar callers' whinnies (10 trials)	7	8	1	3	0	0	0	0	0	0

The number of calls given per individual, and the latency to respond to playback of strangers' calls were not significantly different between morning and afternoon (Mann-Whitney adjusted for ties, W=55.5; p=1; W=28; p=0.5, respectively). The responses *give whinny*, *approach*, *look speaker* and *scan* in the strangers' playbacks, and *look speaker* and *scan* in the familiar callers' playbacks were also not significantly different between morning and afternoon (Fisher Exact tests).

The location of the playback trials (i.e. sleeping site or feeding tree) might be expected to influence responses to strangers' calls. No significant effect was however found either on the number of calls given per individual or on the latency to respond to playback of strangers' calls (Mann-Whitney adjusted for ties; W=69; p=0.93; W=52; p=0.62, respectively). No further statistical tests were appropriate.

The presence of a male or female stranger has very different consequences for the monkeys, so the sex of the 'stranger' playback may influence the response. In fact, there was no such effect on the latency to respond (Mann-Whitney adjusted for ties; W=19; p=0.9), or on the responses *give whinny or other type of call*, *look speaker*, *approach*, *scan*, *flee*, *mob*, *congregate or branch shake* (Fisher Exact tests, all non significant). No further tests were appropriate.

The particular location where playbacks were conducted in the spider monkeys' home range was investigated by drawing a map of the spider monkeys' range with approximate boundaries. I estimated these boundaries from the observational data I collected during my study and from data collected by Chapman during a six year study (Chapman 1988b; Fedigan et al 1988). Most trials were conducted in the core area of the home range (central area, where the monkeys spent most time). The few trials in which stranger' *whinnies* were played closer to the territory boundaries did not provoke any stronger response than trials in more central locations.

7.4. DISCUSSION

The results of the present study do not unequivocally demonstrate that spider monkeys can differentiate between calls given by their own community members and those given by strangers. Receivers showed qualitative variation in response between playbacks: the only instances involving agonistic behaviours, described as specific to intercommunity encounters (*mob*, *congregate* and *branch shake*; Klein 1972), occurred in two trials when the monkeys heard a stranger calling in their range. These two cases involved the largest subgroups that

experienced playbacks, so it is tempting to explain their mobbing response as simply a consequence of subgroup size; but in general the size of the subgroup hearing the call had no effect on the vocal responses response. In general, the number of vocal responses given was remarkably independent of other factors: no variation was found with the activity in which the hearers were involved, the sex of the caller, or the location and time of day of the broadcast. In the quantitative terms of calls given per individual, spider monkeys showed no difference in response between stranger and familiar playbacks. However, in terms of whether a subgroup as a whole gives any *whinny* call in reaction, a response was more likely to a stranger playback, even when trials with unusually large or small target subgroups were discounted, such that target subgroups were exactly the same average size in the two cases.

Before considering the implications of these findings, one must rule out the possibility, as I did in Chapter 4, that they are an artifact of particular acoustic features of the stimuli used in the playbacks or the fidelity of the equipment. I investigated three likely 'contaminating' factors namely, call duration, playback distance, and the filtering used to improve some recordings. Where there were sufficient data, neither the length of the calls selected nor the distance of the speaker significantly effected the responses (the analyses were conducted in the same way as in Chapter 4 so they are not presented here; only the effect of filtering will be analyze since it was not investigated in Chapter 4).

Some *whinny* samples (n=4) had to be filtered in the process of editing due to background noise, a process which might have resulted in a modified call which may be perceived differently from the same non-filtered call. In order to test if filtering affected the responses of the receivers, responses were compared between trials in which filtered or non-filtered *whinnies* had been used. There were no significant differences between filtered and non-filtered calls in the total number of calls given or in the latency to respond (Mann-Whitney adjusted for ties; W=218.5; p=0.08; W= 51.5; p=0.53). The same was the case for those all responses that could be tested: give whinny, look speaker, flee and scan (Fisher Exact test, all non significant).

Therefore, such differences that I found in reaction to playbacks of strangers and familiar individuals can be considered real.

Most strikingly, however, the effects of the caller's identity on responses were very small, whereas one might have expected this difference to be an important one for the monkeys. Whether they heard a stranger or a familiar caller, the monkeys' reaction included a similar set of behaviours: looking towards the sound source, scanning in an alert fashion, giving the same call as that broadcast, and sometimes approaching the speaker. These are also the most common responses that spider monkeys give to naturally occurring *whinnies* (see Chapter 4). It is true that my playback simulates only a single stranger, not the chorus of calls to be

expected from a major group incursion. Yet even the intrusion of one stranger into the core of the community range is presumably a surprising and unwelcome event. The question arises as to why the response is not much greater than that given to the everyday occurrence of hearing familiar group members' calls. There are several possible explanations.

Individual discrimination in long-distance communication is problematic because individually distinctive features may degrade (Richards and Wiley 1980). Spider monkeys may not have recognized strangers' calls as such, but simply as calls from conspecifics who might or might not be familiar. Their responses would then reflect uncertainty, rather than aggression to strangers. This explanation is not entirely convincing: only in three of the current trials was the background noise level high, due mainly to wind, and the speaker distance was never more than 150m, well within the range of the maximum distance from which the *whinny* can be heard by humans. The loud calls of spider monkeys, for instance the *whoop* and *wail* calls, are apparently well-adapted to long-distance propagation. It may be that future playback experiments with these calls will elicit clear and marked responses to simulation of intruding strangers.

Alternatively, the muted reaction may be explained by the composition of the subgroup receiving the call. In spider monkeys it is certainly the males who take a more aggressive role in encounters (see Introduction). In most of my playback trials the audience hearing the calls was composed mainly of females. It may be that female spider monkeys have little interest in repelling strangers. However, a differential response might then reasonably be expected on the basis of the sex of the caller, and I found none. It may also be relevant that most of the trials carried out were in the community's core area, whereas intercommunity encounters may generally take place in the boundaries of the territory. Again, this is unconvincing as an explanation of the mild response, since a strong response would be expected to a deep incursion into the range.

At certain times of the year, food dispersion may not encourage defensive responses. All trials were conducted in the wet season, when food was more abundant, and daily ranges were smaller than in the dry season. In Santa Rosa National Park the food is also more clumped in the wet season, when big fig trees allow a large group of monkeys to feed simultaneously. These factors may have reduced the level of competition for food, and made range defence an energetically expensive strategy. A comparable playback experiment in the dry season will be of interest in this regard.

Interestingly, Mitani (1985b) also found a surprising lack of response to playbacks that simulated strangers' calls in gibbons. Indeed, he found no differential response in gibbons to playback of their own, neighbours' or strangers' songs. Gibbons and spider monkeys have similar diets, body size and locomotor patterns; but while spider monkeys live in a fission-

fusion society, gibbons are monogamous, defend small territories, and travel in cohesive groups. Nevertheless, the same ecological explanation suggested by Mitani (1985b) for his negative results (the low frequency of encounters between different communities of the study area) could be used to explain the weak response in spider monkeys to strangers' calling. Chapman (pers.comm.), who studied the same population of spider monkeys as the one used in this study, saw no intercommunity encounter in a 6 years period. In a home range of over sixty hectares (Fedigan et al. 1988), spider monkeys probably interact rarely with other communities. Other populations of spider monkey, in which intercommunity encounters are more common, may respond differently when hearing strangers in their range. Repeating this experiment in different field sites would therefore be worthwhile.

Chapter 8
PREDATION
The reaction of spider monkeys to the sight or sound of predators

8.1. INTRODUCTION

This chapter represents a preliminary attempt to expand our knowledge of anti-predator behaviour in a community of spider monkeys in Santa Rosa National Park. My main interest in spider monkeys' anti-predator behaviour focusses on their alarm call system; how they use their alarm calls and whether they have a distinct type of alarm call for aerial or terrestrial predators, as other species of primates have proved to have (Cheney and Seyfarth 1990; vervet monkeys' alarm calls). I will start by reviewing the existing evidence of predation in this community and in other populations of spider monkeys, and I will briefly summarize current cases of primates' predator call recognition. Then, I will explain the aims I had when I decided to study the alarm calls of spider monkeys and how these had to be limited to the early phases of the study because the first results were not as expected.

8.1.1. Predation in Santa Rosa National Park

In Santa Rosa National Park spider monkeys are potentially exposed to the following predators: Tayra (*Eira barbara*), Boa constrictor (*Boa constrictor*), five species of cats: Margay (*Felis wiedii*), Jaguarundi (*Felis yagouaroundi*), Jaguar (*Felis onca*), Puma (*Felis concolor*), Ocelot (*Felis pardalis*), and several raptors such as large hawks. However, no actual attack on spider monkeys from any of these predators has ever been witnessed. Chapman (pers.comm.) in a 6 year period (36 months of observation) rarely saw any of the feline species and never in the actual study area (although he saw tracks). He saw tayras seven times. During my study I also saw a tayra once in the day light in the moist part of the study area while I was searching for the monkeys, but I could not see any monkeys nearby. Tayras are terrestrial and arboreal foragers and have been seen up to 20m above the ground in the crowns of large deciduous trees (Janzen 1983). Although they could capture a small monkey, such as an infant spider monkey, the only two instances of interactions between tayras and spider monkeys described in the literature do not report any attack by tayras; on the contrary, spider monkeys barked, followed and

chased them away (Eisenberg and Kuehn 1966; van Roosmalen 1980). It is common to see boas in Santa Rosa (two sightings of large individuals, over two meters, in the dry season 1994). Although no instances of boa predation on spider monkeys have been observed, Chapman (1986) reported an episode of succesful predation of an inmature white-faced monkey (*Cebus apella*) by a boa in Santa Rosa. Boas have also been seen attempting to prey on the totally arboreal howler monkey (*Alouatta paliatta*) at the same site (L.M. Fedigan, pers.comm.). Jaguars prey on a wide variety of mammals including monkeys. Jaguars give roaring sounds which consist of a pulsed series of single, deep, hoarse grunts that can be heard for several hundred meters (Emmons 1990) in the day or at night. Both a jaguar and a puma were seen ranging near the study area during the wet season of 1994, when I was conducting my study. Margays, the most arboreal of Neotropical cats, may feed on monkeys, and their tracks are abundant in Santa Rosa (Janzen 1986). Ocelots, of larger size than margays, are the most commonly seen spotted cat. They rarely climb trees, but hunt and capture their prey on the ground (Emmons 1990). No attack of cats on any of the three monkey species has ever been witnessed at Santa Rosa. In the case of the jaguar and maybe the terrestrial ocelot, a possible explanation for this may lie in the fact that Santa Rosa has one of the highest densities of white-tail deer (*Odocoileus virginianus*). Therefore, jaguars and ocelots may prey more on deer or other terrestrial mammals, easier to capture, than on monkeys (specially on the arboreal, highly agile spider monkey). Thus, although potentially dangerous predators, jaguars and ocelots may not constitute a serious threat for spider monkeys at Santa Rosa and actual aggressive incidents are rare.

Aerial raptors do not seem to represent a big danger for spider monkeys in Santa Rosa either since none of the raptors that could catch a prey of their large size are present in the area. One of the only raptors that could succesfully prey on a spider monkey is the harpy eagle (*Harpia harpyja*). Harpy eagles are no longer present in Santa Rosa, although they were in the area 25 years ago (Chapman pers.comm.).

8.1.2. Predation in other sites

In a review chapter about predation, Cheney and Wrangham (1986) noted that arboreal primates seem more vulnerable to raptors than to carnivores, and according to Terborgh (1983), aerial predators constitute the only serious daytime threat to arboreal primates. Nonetheless, an important piece of evidence not to be forgotten is that *Ateles* remains have been identified from feces of two large felids (a jaguar and puma) at Manu National Park, Perú (Emmons 1987).

To date the only reported instance of an aerial raptor's successful predation on a spider monkey is that described by C.Julliot (1994) in which a Crested eagle (*Morphnus guianensis*) captured and killed a young spider monkey (*Ateles paniscus*) in French Guiana. The incident occurred as follows: a subgroup of three spider monkeys (an adult female, a subadult female and an independent juvenile) vocalized, giving *screams* and *wails*, and broke branches when first detecting the eagle flying over their heads. However, they did not show any subgroup cohesion, and left the juvenile alone, unprotected. After a fast and sudden attack by the eagle, in which it successfully caught and killed the juvenile monkey, the two females remained in the place where the juvenile had been captured for more than two hours, screaming loudly. The eagle did not emit any vocalization before or after the attack.

In La Macarena (Colombia), where there is a whole range of primate predators (jaguars, harpy eagles, black hawks, boas, etc.), Klein (1972) not observed any attacks on *Ateles belzebuth,* or find any primate remains in carnivore scats. However, he did witnessed two encounters between spider monkeys and a large hawk and a tayra. In both occasions the monkeys barked at the predators.

In Suriname, where Van Roosmalen (1980) studied *Ateles paniscus*, at least three predators of spider monkeys are present, jaguar, ocelot and harpy eagle. However, he did not observe any predation on spider monkeys and concluded that day-time predation is probably non-existent in this species due to the monkeys' large size and high ability to defend themselves. Surprisingly, when compared to Manu National Park (below), spider monkeys were seen feeding, unperturbed, while a harpy eagle was flying above them.

At Cocha Cashu Biological Station (Manu National Park, Perú) Symington (1987) reported that known primate predators which could potentially prey on spider monkeys were: jaguars, ocelots, harpy eagles, crested eagles, ornate hawk eagles (*Spizaetus ornatus*) and slate-colored hawks (*Leucopternis shistacea*). This assessment depended on estimations based on the weight of the largest prey found in the faeces of the cats (Emmons 1987) and observations of raptors' attacks reported by Terborgh (1983). Moreover, in a four year field study Symington witnessed two incidents in which a harpy eagle was persistently mobbed by spider monkeys. In these occasions the whole group of monkeys gave alarm calls of a type specific to aerial threats (what she called '*hiccups* ') for a considerable length of time, and males lunged at the eagle and threw branches on its perch. Symington noted that adult males played the most predominant role in the aggressive mobbing response, suggesting a possible sex difference in anti-predator behaviour (a claim supported by the following studies: Carpenter 1935; Eisenberg 1976; van Roosmalen 1980).

8.1.3. Alarm calling of spider monkeys in predator contexts

According to Symington (1987), spider monkeys in Cocha Cashu have two acoustically different alarm calls, easily distinguished in the field: one given to aerial predators, *hiccup*, and one given to terrestrial predators, *bark*. Aerial alarm calls are given to eagles or other large birds flying overhead. Terrestrial alarm calls may be given at humans (by unhabituated individuals), large felids, or in response to the alarm calls of a wide variety of terrestrial mammals and birds (peccary, deer, curassows, trumpeters). Although she claimed that these two types of calls were acoustically different, she did not provide any acoustical basis or a description of sonograms of the calls in support of this claim. Moreover, Symington's own definition of the stimulus eliciting terrestrial *barks* is rather confusing, for it includes birds alarm calling. No other author besides her has made a distinction between aerial and terrestrial spider monkey's alarm calls.

Eisenberg (1976) considered the *bark* as an alarm call usually part of the anti-predator mobbing display, given in response to a novel stimulus from which the individual can escape. Both adult males and females may bark, often in duet (one animal barks in the intervals between the barks of the other), attracting other monkeys to the site. He did not make any distinction between *barks* given in an aerial versus a terrestrial predator context.

He described this call as a repetitive loud sound, audible to approximately 500m, with a duration of 0.15-0.5 sec., intervals ranging from 0.17 to 0.60 sec., and frequencies emphasized between 0.6-1.4 kHz. An important fact he pointed out is that the intervals between each *bark* and the length of *barks* can vary as a function of mood shifts on the part of the sender. Therefore, this call represents an example of the importance of temporal patterning as an indication of arousal level.

However, in a comprehensive paper summarizing all existing literature on spider monkeys' behaviour, van Roosmalen and Klein (1988), listed two types of barks: the '*ook-barks*', term first used by Klein (1972), and the '*tschooks* '. Although they did not provide any spectrographic illustration of the calls, their description of them shows that the first correspond to what Eisenberg (1976) defined as *barks*. The second are shorter, usually doubly pulsed, consisting of 1-3 notes, and used when attempting to re-establish contact. Although there is no mention in this list of two distinct alarm barks for different type of predators, it might be possible that these *tschooks* are equivalent to what Symington called *hiccups*. Further evidence of cases of alarm barking when encountering aerial predators is needed to clarify this issue.

8.1.4. Evidence of predator call recognition in primates

It is important for a forest living primate to be capable of recognizing potential predators from their calls before actually seeing them in order to have a better chance of escaping, or to respond on time with anti-predator behaviour such as alarm calling. Alarm calling attracts other individuals to the site to form a mobbing response which might discourage the predator from hunting successfully. However, among primates there are only four studies that provide suggestive evidence of predator call recognition using playback experiments. Symington (1987) conducted 19 trials in which she played harpy eagle calls to wild spider monkeys (at Cocha Cashu) in groups of different size and composition. The results showed that in half of the experimental trials the entire party left the vicinity of a fruiting tree after hearing the raptor's call. The rates of vigilance behaviour increased after all trials. Hauser (1991) found that three species of forest living monkeys (redtail monkey, *Cercopithecus ascanius*; blue monkey, *Cercopithecus mitis*; and red colobus, *Colobus badius*) can recognize the presence of potential predators by hearing their calls. After the playback of known predator's calls they increased their vigilance and scanning rates, and departed from an area of high food density. Moreover, they distinguished between calls of aerial (eagle) versus terrestrial (chimpanzee) predators, by responding differently to them. Although they did not give different vocal responses to the these two predators, they scanned above the horizon after hearing eagle calls, whereas they never did so following chimpanzees' calls. Macedonia (1991), in a study focusing on the acoustic features used by lemurs to discriminate between calls of aerial predators and other environmental sounds, found that semi-captive ringtailed lemurs (*Lemur catta*) responded with anti-raptor responses to the playbacks of aerial raptor calls (two different hawk species). Chapman and Chapman (1996), focussing on the ecological constraints of polyspecific associations in the Kibale Forest, showed that five species of forest primates altered their behaviour after the playback of a known aerial predator. Red colobus, redtail monkeys, blue monkeys, black-and-white colobus (*Colobus guereza*) and mangabeys (*Cercopithecus albigena*) increased the amount of time they spent vigilant and looked into the upper canopy as if scanning for an avian predator, after the playback of a crowned hawk eagle call.

8.1.5. Aims of the study

My original plan to study spider monkey's antipredator behaviour included two phases. In the first phase I wanted to record a big enough sample from different individuals' alarm calls to be able to conduct playback experiments in the second phase of the study. Because I was aware of the potential problem of having only a small number of

spontaneous alarm calls in this population due to the low predation pressure (during a two-year period Chapman et al. (1990) only heard 48 spontaneous alarm call bouts; Chapman 1990c), I decided to create an artificial threatening situation to evoke alarm calls, using two procedures. One consisted of playing back to the monkeys different predator calls, the other of presenting the monkeys with a visual stimulus, a faked predator. Therefore, the aims of the first phase of the study were:

- To collect a sample of alarm calls from identified individuals for future playback experiments.
- To see if spider monkeys have, as Symington (1987) claimed, a distinct alarm call for terrestrial versus aerial predators.
- To discover if acoustic cues are enough to elicit an alarm response in this community of spider monkeys, thus providing further evidence of spider monkey's predator call recognition and evidence for a larger range of predator calls.
- To explore the sexual variation in spider monkeys' anti-predator behaviour.

In the second phase of the study my intention was to use the alarm calls recorded from identified individuals to conduct playback experiments of terrestrial versus aerial predator calls, and investigate if the responses to these differed. Unfortunately, the results of the first phase were not as expected and I did not have enough time to pursue the playbacks using other stimulus. Therefore, only the first phase of the study could be accomplished.

8.2. METHODS

Observational data on spontaneous calling

The methods used to collect observational data and vocal recordings are detailed in chapter 2 (general methods). Basically, each time a bout of alarm calling occurred during a focal animal sampling, I recorded the following information: the stimulus provoking the calls (if identified), the type of alarm call given, the approximate duration of the bout, the subgroup size and its composition, a description of any other behaviour accompanying the calling, and whether the calling attracted other monkeys to the site.

Predator playbacks

Study site

Experiments were conducted in Santa Rosa National Park during the wet season. A complete description of the forest can be found in chapter 2 (study site). Only one trial of a

playback experiment was conducted with a different community of spider monkeys, a community of six individuals in Playa Nancite, a small patch of riparian evergreen and mixed forest located 17km from the main study area.

Stimuli

Two of the stimuli used for the playback were high quality recordings from the British Library of Wildlife Sounds, London. The first, a jaguar roaring (5 sec. duration), was recorded in London Zoo from an adult male, isolated from its companions, pacing up and down the cage. The second stimulus was a harpy eagle cry (2 sec. duration) recorded in Rio Grande, Venezuela from an adult individual sitting by the nest. The third was a recording of a spontaneous loud cry of a raptor (0.72 sec.) in the study area, a perched hawk (I could not identify the species), which had provoked a strong reaction and alarm calling in a subgroup of spider monkeys nearby (6-5-94). I predicted that spider monkeys would respond to the jaguar and harpy eagle as potential predators, because even if there are no longer harpy eagles in the area (since 25 years ago) monkeys may still recognize its calls as potentially threatening raptor's calls. I also expected the hawk cry to elicit an alarm response since the call was recorded in a natural situation in which its repetitive calling triggered a strong reaction from the monkeys. These calls were prepared beforehand in an endless tape, and the volume of the speaker was adjusted to estimated natural levels for jaguars' roars and raptors' cries, far away from the study area. The equipment used for the playback was the same as the one used in the experiment of Chapter 4.

Procedure

Two trials with a jaguar roaring (one played to the Santa Rosa community and the other to the Playa Nancite community), one trial with a harpy eagle call and one with a hawk call (both to the Santa Rosa community) were conducted. Two observers participated in the experiment. My assistant was responsible for setting up the equipment and playing back the call, while I recorded the vocal and behavioural responses of the monkeys. The target group selected was always a subgroup of spider monkeys that was eating in a fruiting tree. We arrived at a fruiting tree that the monkeys were bound to visit that day, set up the equipment and waited for their arrival. The experiments aimed to represent the most realistic situation as possible. The jaguar roarings were played back almost at dusk with the speaker hidden in the ground, under some bushes. Both the harpy eagle and the hawk were played back from a speaker hidden in the foliage of a tree, raised with a rope 10-15m above the ground. Once a subgroup of identified monkeys arrived, started feeding and stayed in the tree for at least five minutes, we got ready to start a trial. If after a period of one minute none of the monkeys had moved away from the tree or started a chorus of calls, we played back the call for the first time. After 10 sec. the call was played again. We then waited 5 min. to play the call two more times, again with a

time lapse of 10 sec. between each call. I used a 10 sec. interval between calls because I considered it would give the monkeys some time to respond.

Data recorded

In each trial I described into a small tape-recorder in a narrative fashion the whole episode, aiming to record the following information:

- date
- location of the playback in the study area
- location of the speaker and distance to the nearest monkey
- time the call was played
- approximate size and composition of the subgroup hearing the call
- time the first individual called
- number of distinct callers
- type of vocalization of as many identified individuals as possible
- approximate duration of the whole calling bout.

The following behavioural responses of the target subgroup were scored:

- Look at the speaker.
- Scanning (the ground or the sky).
- Approach the site (how many subgroups approach and what was the sex of new arrivals).
- Congregate.
- Flee from the site (approximately how many individuals leave and how many stay).
- Mob (sex of the individuals mobbing)

After the last trial was played I followed and recorded behavioural data of the subgroup for a period of 30 min.

8.3. RESULTS

8.3.1. Spontaneous alarm calling of spider monkeys in Santa Rosa National Park

I recorded 24 bouts of spontaneous alarm calling by spider monkeys' subgroups ranging in size from one to eight monkeys, in both the dry and wet seasons (dry season=18; wet season=6).(A summary of these is presented in Appendix III). The duration of these bouts varied from three seconds to 40 min (average=12 min; N=18 bouts

for which duration could be noted). Table 8.1. presents a summary of the different stimuli triggering these spontaneous alarm calling bouts.

On the six occasions in which the stimulus triggering the alarms were the observers, the calls were given by unhabituated individuals during the first months of the study, when they saw us for the first time that day or we had started following a subgroup.

In one instance (6-5-94) the stimulus triggering a long (14 min) and repetitive alarm calling bout was a raptor, a big unidentified hawk. Although hawks have not been seen attacking monkeys in the park, individuals of this size could potentially capture an infant spider monkey. On this occasion I was observing and doing vocal recordings of an adult female and her juvenile son who were eating peacefully in a tree, when suddenly, only 20 meters away from them, a perched hawk emitted a loud cry. Immediately, the adult female scanned intensely towards the hawk and began to give loud *barks*, sounding very similar to a hiccup (possibly the same type of alarm call that Symington 1987 described as *hiccups*). The hawk gave nine cries during this bout, scattered between the females' *hiccup barks* (see figure 8.1., sonogram with sequence of the hawk first cry and the female's alarm barks). After approximately 4 minutes, other spider monkeys who probably heard the female's calls started congregating at the site and joined her in the barking. Some individuals, not visible, also gave *whinnies* in response to the adult female's barks.

The type of alarm call most commonly heard in all the 24 bouts was the so called 'terrestrial alarm call', i.e. *bark*. Although not all bouts could be tape-recorded, several sonograms of good quality recordings of these *barks* (see figures 8.2. and 8.3.) have similar characteristics (duration, fundamental frequency range, interval between calls) as the ones described by Eisenberg (1976) for this type of call. In the instances in which I could identify the stimuli eliciting these calls, the cause of the barking was either the observers, terrestrial mammals fleeing, or small birds (not raptors) alarm calling (e.g. a crested goan calling). This confirms the contexts described by Syminton (1987) for the same type of call (she included birds calling in her category of stimulus eliciting *barks*). However, the hiccup sounding call was only given in five instances. Four of these were caused by big raptors flying by (not identified) or calling (see instance of hawk calling described above and sonogram in figure 8.1.). The fifth hiccup sounding bout was directed to the observers.

Table 8.1. Summary of stimuli eliciting 24 spontaneous alarm calling bouts

Unidentified stimulus	Observers	Terrestrial mammals alerted by observers	Aerial raptors flying by or calling	Birds alarm calling
5	6	4	5	4

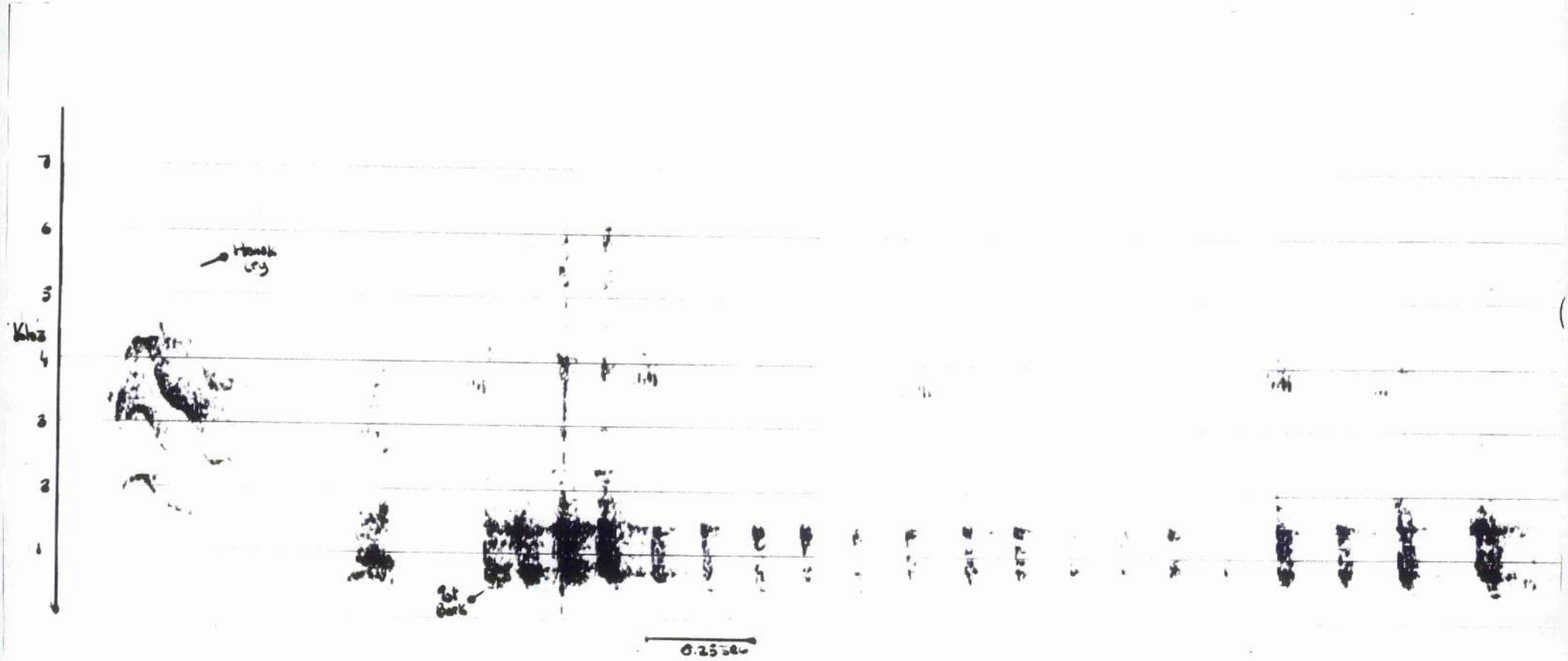

Figure 8.1. Sonogram of an alarm barking bout triggered by a hawk cry (the whole bout lasted 4 min.; date: 6-5-94). These hiccup sounding *barks* were given by an adult female who was feeding with her juvenile son when the hawk started crying. As she was becoming more aroused the barks became doubly pulsed.

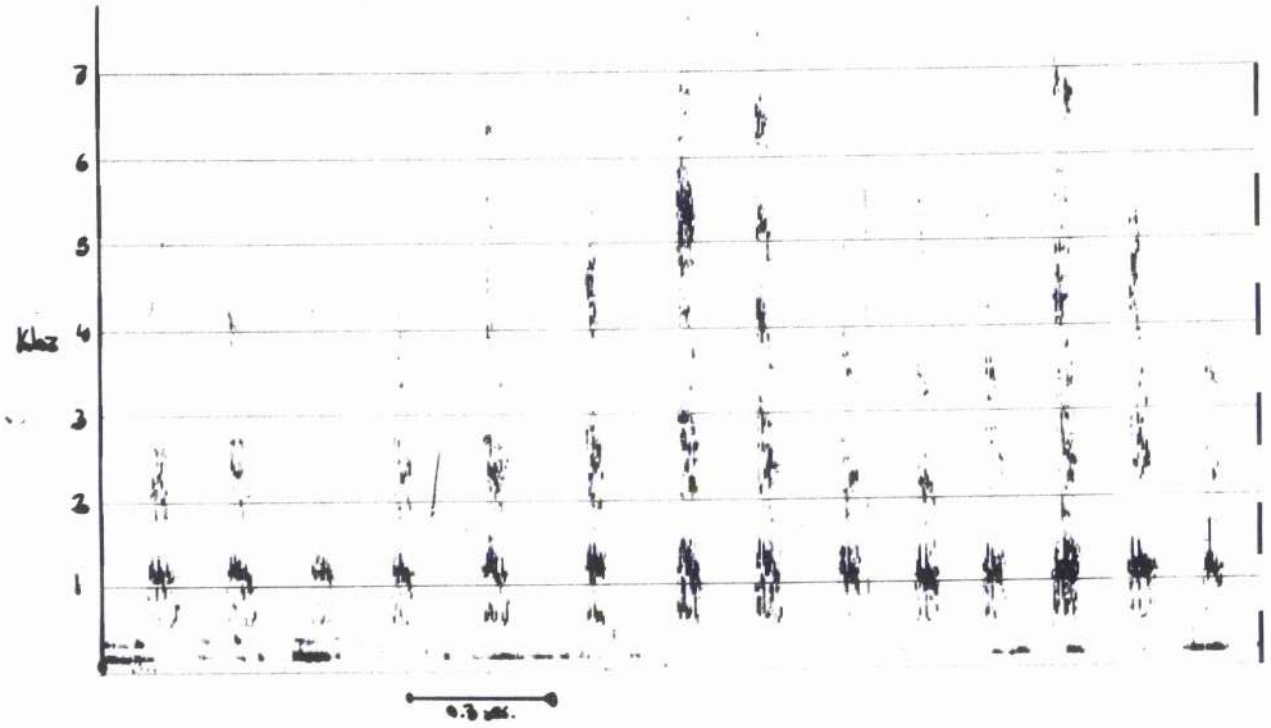

Figure 8.2. Sonogram of an adult female's *barks* as she saw a stuffed cat (*Felis tigrina*) in the branch of a tree ('terrestrial *barks*').

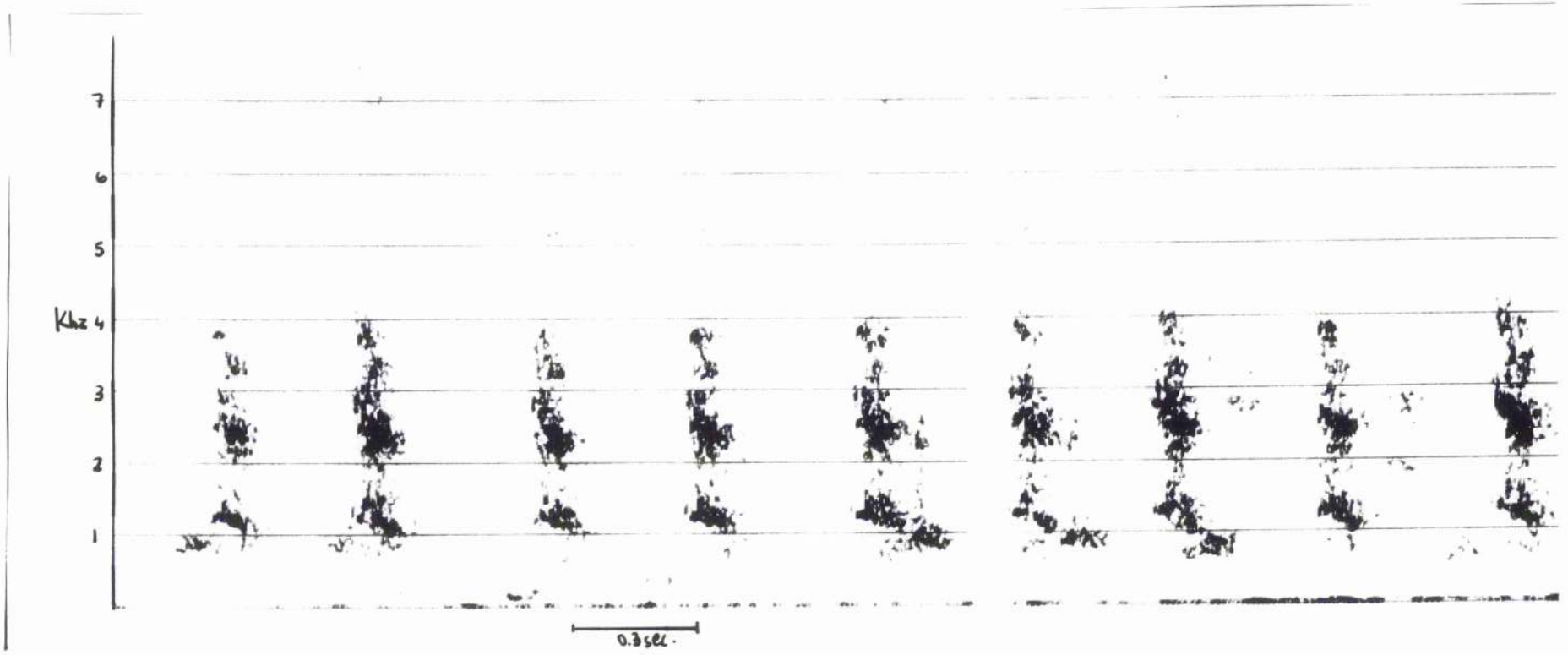

Figure 8.3. Sonogram of terrestrial*barks* given by two subadult females in chorus as a crested goan suddenly alarm called and flew off.

Only in two of these 24 bouts did the alarm calling elicit approach and congregation of other individuals who were in the nearby area. One was the above mentioned episode of the hawk calling. The other took place in the beginning of the study when the barking of a subgroup of eight individuals who were scared by my presence attracted two adult males to the site. They joined the barking and mobbed at me. In all other bouts there was no change in the subgroup size, no individuals joined or were attracted by the calling. Other behaviours often accompanying alarm calling were: scanning, branch shaking, fleeing from the site, mobbing, and throwing small twigs and fruits by moving branches aggressively. Table 8.2. summarizes their occurrence in relation to the stimulus which provoked them. Mobbing displays and throwing twigs occurred only in two instances, mainly performed by males against the observers when the subgroup was large and we had made the first contact of the day with them. In four occasions the monkeys fled and left the site (two after a pigeon and a crested goan alarm called and flew away; one after an unhabituated female saw one of the observers; one for unknown reasons).

8.3.2. Predator calls playbacks

Since I only conducted one trial with each predator call (except for the jaguar call which was played to two different communities of spider monkeys), no formal analyses were performed. I present a transcription, describing how the monkeys reacted to each playback, with the most salient responses underlined.

Jaguar playback experiments

1st Trial (29-5-94): Santa Rosa community

"It was 5.29pm when we set the equipment on the junction of two trails where there were a few trees of 'Pochote' (*Bombacopsis quinatum*) flowering. I had seen the monkeys passing by this spot and stopping to eat the flowers of these trees. Therefore, I thought it would be a good place to wait for their arrival. The speaker was hidden under low shrubs 10m away from us. Even though the sun was almost set, visibility was still good. After a few minutes, we saw a group of nine monkeys approaching the site. They split off in two subgroups as they entered the biggest tree and started eating flowers. Five monkeys were eating 15m away from the speaker: an adult male, a subadult male, an adult female with her infant and two subadult females. This was the subgroup on which I was going to focus for my recordings of behavioural and vocal responses. As they continued eating, we broadcast the roaring of a jaguar. Immediately after the roaring, a howler monkey (which we had not seen before) howled loudly, two spider monkeys gave loud *whinnies*, and one subadult female stopped eating and scanned around. The rest of the subgroup continued eating. After 10 sec. the roaring was played back a second time. A howler replied immediately with a deep wail. After 6 sec. all the monkeys stopped eating and looked towards us, alert; a subdult male gave a *whinny*. The adult male remained alert for 12 sec. after the playback. He scratched once, but then resumed his eating

activity. We waited for 5 min. before playing the call two more times. The response to these was basically the same as to the first two: the howler monkey howled loudly, and 4 spider monkeys gave loud, *whinnies*. This time however, the *whinnies* were answered by individuals of another spider monkey subgroup feeding in a tree 20 m. away from the target subgroup. The behaviour of the spider monkeys seemed to be more a reaction to the howler monkey's calls than to the jaguar's roaring, as spider monkeys often give *whinnies* after hearing a howler monkey's call."

2nd Trial (31-8-94): Playa Nancite community

" At 5.17pm we set the equipment near a 'Guarumo' tree (*Cecropia peltata*) 15m away from a subgroup of three spider monkeys. These were part of a community of six individuals who live in this small patch of forest. Two of them, an adult female and a subadult male, were foraging in the tree, while the third, an adult male, was resting. The rest of the community was scattered around foraging out of sight at a distance of approximately 50m away from us. The vegetation around us was not very dense, so the visibility of the monkeys was good. After we played back the jaguar roaring for the first time, the adult male was alert, scanning the ground, but the other two ignored the call and continued foraging. After the second time the call was played, the monkeys were resting on a branch in the same tree and did not respond at all. We waited five minutes to play the call two more times. After the third time, the adult male looked to the ground, but there was no response from the others. After the last time the roaring was played, the adult male gave a soft *whinny* and looked towards us while resting with the other two. In the nearby area (within hearing distance), there was a group of white-faced and howler monkeys who did not react in any way to the playback."

Harpy eagle playback experiment

Trial date: 5-7-94. Santa Rosa community

"2pm. We set up the equipment near a group of fruiting trees ('Mora', *Chlorophora tinctoria*) at which the monkeys had eaten the day before. The trees were high (25m) but did not have dense canopies, so the degree of visibility was fairly good. As we were waiting, a group of howler monkeys arrived and started eating fruits. At 3.45pm, the howlers moved away from the trees as a subgroup of eight spider monkeys approached the trees. They gave *whinnies* and began to eat. Some of the individuals I could identify were two adult females with their infants, a subadult female, a subadult male and a juvenile male. The speaker was 15m away from them. After things had calmed down, that is after all the monkeys had entered the tree, had stopped giving *whinnies* and had been feeding for 10 min, we started the trial. After a minute passed a harpy eagle cry was broadcast. All visible monkeys stopped eating, looked to us and scanned towards the speaker in an alert fashion. After the second time the cry was played, an adult female grabbed her infant who screamed as her mother pushed her towards her belly. All of the subgroup began to move out of the tree, fleeing hurriedly and still scanning towards the speaker. As they were moving away, two individuals gave locational *whinnies*. I followed them while my assistant stayed at the site to play the call two more times. During the 5 min. lapse before the call was played, they moved approximately 30m away from the playback site and foraged. After the third and fourth repetitions of the call, a howler howled and two spider monkeys of the subgroup I was following gave *whinnies*, as they continued moving away further from the site. I stayed with them for 20 min. until they entered a fruiting fig tree and split in two."

Table 8.2. Summary of responses given to each stimulus in spontaneous alarm calling bouts

(frequency does not appear, only whether the response occurred or not)

		Responses						
		Approach	Congregate	Scan towards ground	Scan towards sky	Branch-shake	Mob	Flee
Stimuli	Unidentified stimulus			*		*		*
	Observers	*	*	*		*	*	*
	Terrestrial mammals alerted by observers			*		*		
	Aerial raptors flying by or calling	*	*		*			
	Birds alarm calling							*

Hawk playback experiment

Trial date: 17-8-94. Santa Rosa community

"At 7.42am we set up the equipment for doing a playback experiment with a hawk call which had provoked a strong reaction from nearby spider monkeys when we recorded it in Santa Rosa. We chose an area of open vegetation near the campsite where a big tree 'Jobo' (*Spondias mombin*) was fruiting. A subgroup of males had been feeding in that tree the previous morning, so we hoped that they would also visit the tree that day. At 8.02am a subgroup of 4 monkeys arrived and entered the tree, giving feeding *whinnies*. Two of them were the same adult and subadult males that we saw the day before in the tree; the other were two subadult females. As they entered the tree, the adult male displaced one of the females from a branch; she moved away from him quickly, giving a *whinny*. The distance from the speaker to the nearest individual was 10m. We waited 5 min before starting the trial. After one minute of the start of the trial we played the hawk call for the first time. All the monkeys continued eating, but one of the females gave two *whinnies*. After the second repetition of the call, three of the monkeys stopped eating and looked towards the speaker. The subadult male branch-shook, looked towards the speaker, approached the adult male and put an arm around him. They affectionately embraced each other, as a form of reassurance behaviour, and gave trills. Both males were alert with their tails entwined. The fourth individual, a subadult female, continued eating fruits in the opposite side of the tree. During the next 5 min., they resumed their eating activity, giving feeding *whinnies*. After the call was broadcast for the third time, the subadult male gave *squeals*, jumped out of the tree and moved away from the area followed by one of the subadult females. The adult male stopped eating and was alert. When the call was played a fourth time, the adult male and female looked towards the speaker, and continued eating. They stayed in the tree for 12 minutes and began moving away following in the direction of the other two."

The results of playing recorded predator calls were somewhat disappointing. Neither the roaring of a jaguar, nor the piercing cry of a harpy eagle, nor the call of a local hawk elicited a single alarm call from spider monkeys. The last of these evoked the strongest reaction: although it was not a dramatic response, one of the males gave some *squeals*, typical of stressful situations, approached the other male seeking reassurance, and finally left the fruiting tree hurriedly. However, two monkeys continued eating calmly in the tree for a substantial amount of time.

8.4. DISCUSSION

A close look at the responses given to the playbacks of predator calls shows that the reaction of the monkeys was not exactly the one to be expected when monkeys detect potentially dangerous predators in their range. No alarm calls were recorded. Two responses which occurred in all trials were to look at the speaker and give *whinnies*. Scanning of the ground occurred only in the two jaguar playbacks, but scanning of the sky did not occur in any of the aerial predators' playbacks. However, in the case of the first trial of a jaguar playback, the response of the monkeys seemed more a reaction to a

loud howler's howl than to the actual jaguar's roaring. The fact that spider monkeys often give *whinnies* after hearing loud noises (even to unfamiliar sounds such as that made by a truck passing in the nearby road) leaves open the possibility that in this playback they did not recognize the jaguar call as belonging to a predator but just as a sudden unidentifiable noise to which they responded by giving *whinnies*. Indeed, a possible explanation for the weak response found in all trials could be that the recordings did not represent a sufficiently realistic jaguar roaring or harpy eagle cry. Chapman (pers. com.) tried broadcasting jaguar and harpy eagle calls to the same population of monkeys but got no response from them: the animals looked towards the speaker, but did not call or move. He suggested that the explanation for this may have been that the recordings were not of high quality (Cornell Sound library). The same problem could be responsible for the results of this study. The small number of trials conducted and the lack of a strong, uniform response to the playbacks makes it rather difficult to draw any decisive conclusions with respect to the ability of this community of spider monkeys to recognize predators from their calls.

However, if acoustic cues were not enough to elicit a vocal alarm response in this community of spider monkeys, would the sight of a predator have provoked a stronger reaction from them? I had the opportunity to use two stuffed cats, so I decided to do two pilot trials with them because I wanted to compare the reaction of the monkeys to visual versus auditory cues, and to tape-record a sample of alarm calls from spider monkeys which could then be used in further playback experiments. Stuffed predators have been successfully used before in experiments with primates (wild chimpanzees, Kortland 1972; ringtail lemurs, Pereira and Macedonia 1991) in order to provoke responses similar to encountering a real predator.

Two stuffed cats, an ocelot and a margay, were obtained from the Museo de Historia Natural of San José and the Universidad Nacional de Costa Rica. I followed an *ad libitum* procedure which consisted of placing the stuffed cat high up in the branch of a big fig tree that was fruiting and was visited daily by the monkeys (see plate 8 of stuffed margay in the branch of a tree). We waited in that fig tree until a subgroup of monkeys arrived and saw the stuffed cat. Only two trials were conducted, one with each cat, to avoid the possibility of habituation. Trials were over a month apart, and the identified monkeys that saw the margay in one trial were not the same that saw the ocelot in the other trial. When the monkeys arrived at the tree I recorded their calls, and in the ocelot's trial I video-taped the whole sequence, while my assistant counted the number of monkeys arriving and noted the composition of the subgroup. Special attention was placed to scoring the sex of the individuals participating in mobbing the stuffed predator.

Plate 8. Stuffed margay (*Felis wiedii)* placed 10m above the ground, in the branch of a fig tree.

Margay trial: 6-9-94

"After waiting for four hours in a big fruiting fig tree near the tree in which we had placed a stuffed margay (10m above the ground), two spider monkeys, an adult female and her juvenile son, arrived. As the female was entering the fig tree, she saw the stuffed cat from a distance of 20m and started giving typical spider monkey's terrestrial alarm calls (i.e.*barks*). These *barks* were repetitive and had a short interval between them. They seemed to change as a function of the female's arousal level (i.e. as she approached the tree where the cat was, the *barks* were given at shorter intervals and higher speed). Alarm calls continued to be given for the entire 20 min. period that the female stayed in the area; she never ceased staring at the stuffed margay. During the episode, she branch-shook once looking towards the cat, but never got closer than 15m from it. The behaviour of her juvenile son was rather different, for he did not give any alarm call. Seemingly unafraid, he curiously approached the cat and came within 20m of it. He glanced at the cat and returned to the fig tree to eat. While he was eating, I could hear him giving soft *whinnies* sporadically. His mother paused from her continuous barking only once, to reply to her son's *whinnies* with a *bark* graded into a *whinny*. After 20 min the female slowly started to move away from the site, still barking softly. She was joined soon after by her son."

Ocelot trial (video-taped): 12-10-94

Ocelots have a bigger size than margays but they rarely climb trees. For this reason I made a few attempts to place the stuffed ocelot in the ground near the fruiting trees in which I knew the monkeys would eventually feed. However, all of the trials were unsuccessful because the monkeys never saw the cat in the ground. Therefore, I decided to place the ocelot in a tree branch not too high up above the ground.

"We arrived at the site at 8.30am and placed the ocelot 9m above the ground in a big fruiting fig tree, under some leaves. Spider and other monkey species had been visiting this tree almost every day that week. While we were waiting for spider monkeys to arrive a group of white-faced monkeys entered the tree and saw the stuffed ocelot. A few males and a female approached to within 6m of the stuffed cat, giving alarm calls and shaking branches. This behaviour continued for about 15 min. after which they left the area. At 11.05am, from the hill on which we were stationed we heard spider monkeys calling from 300m away. A subgroup of five spider monkeys, an adult male, a subadult male, an adult female with her infant and a juvenile female, entered the tree. At first, the monkeys started eating fruits without noticing the stuffed cat. The adult male gave a *whinny* to which two individuals responded with *whinnies* of their own. When the juvenile female jumped on the branch where the adult male was eating, he chased her away from the branch. After 7 min of the monkeys' arrival, the adult male who was closest to the cat, saw it. He immediately started giving alarm *barks* and *squeals*, and launched himself to within 8m of the cat. He began branch-shaking and jumping-up and-down. The subadult male quickly joined him. Together they began a mobbing display. Barking loudly, they branch-shook in order to drop twigs upon the stuffed predator below. Meanwhile, the adult female screamed and barked when she saw the cat but stayed high up in the crown of the tree next to her infant and juvenile daughter, who was also barking. All four individuals were scanning vigilantly towards the cat the entire time. After 30 min of discovering the cat all the monkeys were still barking but not as intensely as before, and intermittently began eating fruits again."

The reaction of spider monkeys to the sight of an actual predator (stuffed) was stronger than the one given to predators' calls. Alarm *barks* were given by almost all members of the two subgroups which discovered the predators. When a large subgroup of spider monkeys found, as they were feeding, a stuffed ocelot in a branch of the fruiting tree, the males started a strong mobbing response against the cat while the females and an infant stayed in the rearguard. Thus, the males played the most active role in the anti-predator response, confirming the idea present in the literature (Symington 1987; Fedigan and Baxter 1984) that in this species males have a decisive role in the predator context, forming for example cooperative mobbing responses. In two of the spontaneous bouts of alarm calling recorded during the study, mobbing displays were performed only by males.

A possible explanation for the differential reaction provoked by the two stimuli (auditory versus visual) may be that the actual threat of predation in this community is very low. Thus, it may not pay to this population of spider monkeys to spend a high amount of energy in mobbing or alarm calling to invisible predators: they may need to see, not just hear, the predator to engage in such a costly behaviour as is a mobbing display. It would be worth conducting these playback experiments at a time when the density of predators in the park is higher. For example, because of the high amount of rain fallen during the year 1995 in Santa Rosa National Park (pers. comm., Róger Blanco) there was more food, more mammals and the number of sightings of felids (jaguars and pumas specially) in the park rose considerably (three sightings of a jaguar in one month). It would be worth replicating the experiments doing a higher number of trials under these different circumstances to see if the responses to the predator calls were then stronger.

Next, I will discuss whether my observational data supports Symington's (1987) claim about the existence of two different alarm calls, one for aerial predators and one for terrestrial ones; in doing so, I will try to integrate the terms that have been used in the literature to refer to apparently different alarm vocalizations. Two different sounding types of alarm calls were given in my study. The most common one was the terrestrial *bark*, which was given in the same contexts as the ones described in other studies (Eisenberg 1976; Symington 1987). The 'aerial' *hiccup bark* was mainly elicited by aerial stimuli, i.e. raptors flying by, but also, in contradiction with Symington, by observers. There does not seem to be uniformity in the category of stimulus eliciting these *hiccup barks*. Moreover, a visual inspection of the sonograms of the two calls does no show any obvious acoustical difference (although acoustic analysis will have to be done). Therefore, Symington's (1987) claim that spider monkeys have two distinct alarm calls, aerial versus terrestrial, seems unlikely to be true in this population. Based on the observational data in my study and descriptions in the literature, what Symington called *hiccups* may be equivalent to the *tschooks* described by van Roosmalen and Klein (1988) as calls used to re-establish contact. These are not predator-directed or part of a mobbing display, as the *bark* might

often be, but are used when the monkeys find any stimulus (familiar or novel) which causes uneasiness, or confusion. Thus, the *hiccups* of the adult female after the hawk cried may not have been given against the predator but to attract others to the site (which she in fact did). In this sense the *hiccup bark* would function more as a sort of long call. In fact, in a few instances I heard this type of *bark* from monkeys travelling on their own who were trying to re-establish contact with other conspecifics, when there was not any apparent sign of predators nearby. My opinion is that these *hiccups* or *tschooks* do not function specifically to designate the presence of an aerial predator, but rather they refer to a wider range of stimuli, and are used as advertising signals to establish contact with other spider monkeys.

Finally, if we consider the issue of having different alarm calls to designate different types of predators from an evolutionary perspective, it does not seem adaptive for an arboreal species such as the spider monkey to have two functionally different alarm calls. According to Macedonia and Evans's paper (1993), the major selective force in the evolution of predator-class-specific alarm calls is the incompatibility of responses required by different predator classes. Thus, terrestrial species such as vervet monkeys and ringtail lemurs have to respond to raptors and carnivores in two planes (ground and trees), in ways that are frequently opposed. They have developed functionally referential antipredator calls. In a species as arboreal as spider monkeys (as it is the case for ruffed lemurs, mentioned in the same paper), the response options for escaping an aerial versus a terrestrial predator are not entirely opposed to each other, and take place in the same plane. Individuals may respond to terrestrial predators by barking and mobbing. When they detect a raptor they may also bark and mob, but rapidly flee and move into the canopy of a tree. Moreover, aerial predators clearly represent a bigger threat than terrestrial ones since spider monkeys rarely come to the ground. In this species' predator context there does not seem to be a strong need for selection of a predator-class-specific alarm call system. However, further playback experiments need to be done to support these tentative considerations.

Chapter 9
Discussion

In this discussion chapter I will first summarize several significant results found in the thesis, putting them in relation to my predictions and to the few previous studies on the topic of vocal communication of spider monkeys. Then, I will list the points that remain unanswered and how future research may shed more light on them. Results related to more broad theories of vocal communication will be dealt with in the conclusions' chapter at the end of the thesis, integrating them with results of the captive study on chimpanzee's vocal communication.

During the year 1994 spider monkeys in Santa Rosa National park were observed feeding on a wide variety of species and types of food, most of which coincide with the diet described by Chapman (1988b) for the same community, i.e. *Ficus, Masticodendron capiri, Dipterodendron costaricensis* and *Pithecellobium saman*. However, the trees in which the monkeys seemed to give more calls (*whinnies*) were certain individuals of species which held the largest crop of fruit, able to sustain a large group of monkeys eating (e.g. *Bombacopsis quinatum*), raising the possibility that some *whinnies* might convey information about food (e.g. food abundance). The location of these particular individual trees influenced the daily itineraries of spider monkey subgroups, whose size averaged four monkeys during the study period. During ranging and foraging, spider monkeys fissioned in small subgroups of variable sizes, spread out from each other, communicating by giving *whinnies* which were often answered with the same call by conspecifics out of sight from the caller. Thus, individuals could potentially keep track of the location of other conspecifics while foraging or travelling between feeding sites. Sometimes an adult female led the way as if she followed a predetermined foraging route to the better quality and more abundant food sources.

Although the *whinny* vocalization was most commonly heard in foraging contexts, it was also emitted under varied social circumstances, e.g. when subgroups met, when subgroups entered a sleeping site for the first time, when monkeys were travelling from one foraging area to the other, etc. I compared the frequency of different responses given to *whinnies* emitted in different contexts. Spider monkeys responded significantly differently to *whinnies* given by conspecifics in four selected contexts (locational, resting, feeding and detecting an observer for the first time). *Whinnies* given in locational contexts provoked an active response from hearers (i.e. give a *whinny* back or approach) more often than those given in feeding or resting contexts. *Whinnies* caused by the sight of an

observer were never responded to in any particular way. Moreover, playback experiments confirmed the existence of two functionally distinct *whinnies* in the spider monkey repertoire, a locational *whinny* and a feeding *whinny*. After hearing a locational *whinny* the monkeys responded more often by 'whinnying' back, whereas they scanned more after feeding *whinnies*. Thus, the first *whinny* may function as a position indicator in social contexts, while the second may be a generalized food call, associated with a broad category of foods (e.g. a tree with ripe fruit, flowers or leaves).

Acoustic analyses of the *whinny* call concentrated on the variation of several acoustic features between individual monkeys' calls and on structural differences of *whinnies* given in two different contexts. Although on the whole, *whinnies* produced in feeding contexts were not acoustically different from those produced in locational contexts, for several particular individuals, the feeding/locational distinction was clear; however, the acoustic features which distinguished one context from the other were specific to a particular individual, not common to all spider monkeys. The acoustic feature which best discriminated between feeding, locational and resting *whinnies* in each of the three females tested was the number of frequency modulations or arches in the call. Thus, in all three females locational *whinnies* had a fundamental frequency with more arches or modulations than feeding *whinnies*. Analyses of individual differences in spider monkeys' *whinnies* found what other studies (Chapman and Weary 1990; Masataka 1986) had previously found, i.e. that several acoustic variables differed significantly between individuals.

A review of the literature on the subject of intercommunity encounters in fission-fusion species showed common aspects in the behaviour of several species (chimpanzees, spider monkeys, pygmy chimpanzees, woolly spider monkeys, red colobus). Intercommunity encounters in these species were characterized by the active role played by males, who cooperate with each other in territorial defence. The level of physical aggression was mild in spider monkeys when compared to that shown by chimpanzees, being limited to mobbing behaviour and an occasional wound injury. The common factor which seemed to drive males of these species to act aggressively during intercommunity encounters was the access to females as reproductive resources and the monopolization of large food sources. Although no actual cases of intercommunity encounters were observed during my one year study, the use of two indexes of defendability (Mitani and Rodman 1979; Lowen and Dunbar 1994), based on the notion of territory as defended space, allowed me to confirm that spider monkeys can monitor the boundaries of their range and act territorially. However, it would be advantageous in these intercommunity encounters to be capable of detecting 'intruders' by their vocalizations. Playback experiments of stranger *whinnies* versus familiar individuals' *whinnies* showed that spider monkeys do not seem to discriminate between strangers and familiar individuals by their calls alone. Although behaviours described in the literature as typically occurring

during intercommunity encounters, i.e. mobbing, branch-shaking, and barking, took place after playbacks of a stranger call but not after playbacks of familiar individuals' calls, in other ways spider monkeys behaved similarly after both type of playback, i.e. looking towards the sound source, scanning, approaching the speaker and giving a *whinny* back. Moreover, a vocal response was more likely after hearing a stranger call than a familiar individual's call. It is possible that if a call more common of intercommunity encounters, i.e. the *whoop* or *bark* (Klein 1972) was used the reaction would be more dramatic.

The existence of acoustic individual differences in the *whinny* provide support for the potential existence of vocal recognition in this species, at least at the level of familiar individual calls within the same community. However, the results of strangers versus familiar individuals playback experiments, i.e. that spider monkeys do not discriminate between stranger and familiar *whinnies*, question that vocal recognition between individuals of different communities exist.

Although a number of potential spider monkey predators are present in Santa Rosa National Park, the instances of observed predator attacks in this population are scarce. For this reason I used several methods to try to elicit bouts of alarm calling and other anti-predator behaviours from the monkeys. Whereas playbacks of the calls of different predators (roaring of a jaguar, the cries of a harpy eagle and a local hawk) did not provoke a strong response, the sight of a stuffed predator did. In the two occasions when different subgroups of spider monkeys saw the stuffed predator they alarm barked, mobbed and branch-shaked. The alarm calls given, i.e. *barks*, were those typically given when encountering real predators. The males were the ones that played the most active role in the anti-predator response. My observational data on spontaneous occurrence of alarm calling bouts did not confirm Symginton's (1987) claim on the existence of two distinct types of alarm calls, one for terrestrial predators, *bark*, and one for aerial ones, *hiccup bark*. A broad category of stimuli elicited the so called aerial alarm call (raptors and other big birds, observers, a lost individual trying to re-establish contact with other conspecifics). Thus, it is possible that the *hiccup bark* functions to attract conspecifics to the site when a stimulus provoking uneasiness is found, rather than as a predator-associated call. Given the arboreal nature of spider monkeys and the kind of escape responses necessary to flee from predators, it does not seem likely that a predator-class-specific alarm call system would have evolved in this species.

In summary, the main issues on which this thesis has so far focussed are: a) the function of two types of calls in the spider monkey repertoire, i.e. the *whinny* and the alarm *bark;* b) whether spider monkeys have the ability of vocally recognizing individuals' identities by their *whinny* calls, for instance in discriminating familiar individuals' *whinnies* from those of strangers of another community; c) what information feeding and

locational *whinnies* and alarm barks communicate to other monkeys, and whether either of these calls can be considered as referential signals; d) the ability to recognize predators by their calls. The question of referential signalling will be dealt with in the conclusions chapter.

The only other study that has investigated the function of the *whinny* call is that conducted by Chapman and Lefebvre (1990) with the same population of spider monkeys. They focussed on the *whinnies* that spider monkeys give when they enter fruiting trees, and found evidence in support of the idea that they function to manipulate the size of foraging subgroups in a way that minimizes feeding competition. My results are complementary to these in the sense that they give additional support to the existence of a feeding *whinny*, which according to the previous authors is correlated with several ecological and social factors, i.e. when fruiting trees were large, when food was abundant and when subgroups contained high-ranking individuals spider monkeys called more frequently. When looking at the results of the two studies together, it can be seen that common responses to this feeding *whinny* were to join the caller and scan in its direction. However, feeding *whinnies* may sometimes elicit no reaction at all (excepting possible subtle changes in gaze or orientation of the body which could not be investigated in detail). In Chapman and Lefebvre's study calling in food trees did not always result in joining (the percentage of individuals joining a caller in a food tree was low).

Chapman and Lefebrve's study did not clarify whether there are other types of *whinnies* besides the one given in foraging contexts. It is possible that in their study functionally different *whinnies* were lumped together into one category. My thesis provides evidence of the existence of a type of *whinny* which had not been described before, one used in locational contexts. This locational *whinny* functions mainly as a sort of deictic signal, to which other individuals often reply by giving a *whinny* back. These two vocalizations, feeding and locational *whinnies*, seem highly adaptive for the foraging strategy imposed by spider monkeys' food sources. Thus, in a species in which individuals spend large amounts of time out of visual contact with each other, and in which the composition and size of subgroups varies constantly, these two *whinnies* allow them to maintain vocal contact with each other, monitoring constantly the position of nearby individuals and possibly informing about the location of food sources.

Future research on the *whinny*, preferably with a larger number of identified monkeys, could concentrate on the following points. First, it will be of interest to conduct further playback experiments with the feeding *whinny* taking into account ecological conditions, such as variation in responses to *whinnies* given when finding different types of food (fruits, flowers, leaves), but also considering social factors such as a possible 'audience effect', e.g. whether females with infants or dependent juveniles call more in feeding trees than females without offspring. Moreover, since the *whinnies* described by

Chapman and Lefebvre (1990) had the potential ability to inform others about food abundance by changing for example the rate with which they were given, playback experiments could be conducted varying the rate of the *whinnies* used as stimulus. Thus, one could study the effect of variation in the rate of delivery on the number of individuals approaching or on the urgency of the approach response. Since resting *whinnies* provoked different responses from receivers, playback experiments with this call and also with *whinnies* given in the three different locational contexts defined in this study may provide evidence of the existence of other functionally distinct types of *whinny*.

No other studies except Eisenberg (1976), Chapman and Weary (1990) and Masataka (1986) have studied in detail the acoustic structure of the *whinny*. Besides confirming what these studies had found, i.e. that there are enough individual acoustical differences in the *whinny*, my thesis described acoustical variation between different types of *whinnies*, discovering that for a given individual one specific feature of its acoustic structure, i.e. number of arches in the fundamental frequency of the call, could be used to differentiate between feeding, resting and locational *whinnies*. Future playbacks could be conducted, synthesising the calls by varying the number of arches in the fundamental frequency to test if they provoke different responses in the monkeys (e.g. a call with more arches may elicit the response of giving a *whinny* back, a response similar to the one given when hearing locational whinnies). However, the call sample I used was small and the most important limitation of my acoustical analysis was the need for lumping into a single category, 'locational', *whinnies* given in three different locational contexts. Future acoustic analyses on the *whinny* should concentrate on investigating subtle acoustic differences between potential variants of locational *whinnies* with a larger sample of calls, and on describing acoustically a larger sample of resting *whinnies*.

In addition, further playback experiments could be conducted with for example feeding *whinnies* of individuals of the same community to obtain more data on whether spider monkeys have the ability of vocally recognizing individuals' identities by their *whinny* calls.

The other call on which my study focussed is the alarm *bark*. Results of spontaneous bouts of alarm calling in my study and experimental evidence in Symington's (1987) work shows that the most likely function of these *barks* is to attract other conspecifics to a site to mount a mobbing response. However, we must consider here the results found in the only other study of spider monkeys' alarm calls, that was carried out by Chapman at al. (1990) with the same community of monkeys. They played known females' *barks* to different size subgroups of monkeys to test if alarm calls function as an honest advertisement of the number of defenders in a group, or whether they serve to warn kin of the presence of a predator. Their results did not support the honest advertisement hypothesis. They concluded that the repetitive calling of spider monkeys when detecting a

predator may function to maintain visual vigilance, and that they alter the duration of their alarm calling in response to the number of kin in the vicinity, increasing the duration of alarm calling as the number of kin in a subgroup increased. Thus, alarm calls in this species may function in three ways: to attract conspecifics to the site, to maintain visual vigilance and to warn kin of the presence of a predator to increase their chances of fleeing. Furthermore, results of this thesis do not much support previous research (Symington 1987) which suggested the existence of two different types of alarm calls for different predators. Further playback experiments should be conducted with supposedly aerial barks and terrestrial barks to test if they provoke markedly different responses.

A related issue is the possible ability of spider monkeys to recognize predators by their calls. Although Symington's (1987) study concluded that spider monkeys could recognize predators by their calls, neither my attempts of playing back recorded predator calls, nor Chapman's, provoked much reaction from spider monkeys in Santa Rosa. However, before reaching a final conclusion about the ability of the monkeys to recognize predators vocally, further playbacks should be done with a more sophisticated equipment, a higher number of trials and a larger number of call types from predators. Moreover, as a way of recording a sample of alarm calls from spider monkeys to use in future playbacks, it will be worth conducting an experiment in which a stuffed predator (a margay or an eagle) were presented to the monkeys together with the predator's vocalization (a margay roar or a harpy eagle cry). In this way one could test if they responded with a different type of *bark* when seeing and hearing an eagle, than when seeing and hearing a terrestrial predator.

The field study presented in the previous chapters allowed me to test several hypotheses about the function of spider monkeys' calls; to explore the way in which they use their vocalizations in an environment subjected to seasonal food variations and variable predator pressure; and to explore how this environment might have moulded their vocal communication system. However, in field conditions it is not always possible to manipulate ecological variables such as food abundance, or social variables such as group composition, that permit to have a closer look at specific factors which may affect call production. In captive studies one can manipulate these kind of variables. In the next part of this thesis I present an experimental study on the food-associated calls of chimpanzees, which have a similar social organization as spider monkeys and also exhibit several parallels in their vocal communication (see chapter Introduction).

Part 2. CAPTIVE WORK

Chapter 10
An experimental study on chimpanzees' food-associated calls: effect of the social audience and the quantity/divivisibility of food

10.1. INTRODUCTION

In both captive and free-ranging environments, when chimpanzees find food they produce calls which attract other conspecifics to the food source. The types of call most commonly associated with food are *rough grunts* and *pant-hoots*. However, while *rough grunts* are very soft calls that only animals nearby can hear, occurring specially when approaching and eating preferred food (Marler and Tenaza 1977; Goodall 1986), *pant-hoots* are long-distance vocalizations given in a variety of contexts, including arriving at a rich feeding site, joining other community members after separation, and during agonistic displays (Goodall 1986). Clark (1991) found that *pant-hoots* given in the context of food were acoustically indistinguishable from *pant-hoots* given in non-food contexts. Thus, the label of 'food call' seems more appropriate for *rough grunts* than for *pant-hoots*, but the former have been less studied in the field because of its short range transmission. Although both types of call are given by male and female chimpanzees of all ages, the rate of pant-hooting is lower for juvenile females than for males of any age (Mitani and Nishida 1993). Moreover, individuals can be distinguished by their *pant-hoots* (Marler and Hobbett 1975), and two studies have shown that high-ranking males give more *pant-hoots* than low-ranking ones (Mitani and Nishida 1993, at Mahale; Clark and Wrangham 1994, at Kibale). There have been several proposed functions for pant-hooting in the wild:

a) intergroup spacing (Goodall 1986)
b) coordination between parties of the same community (Boesch 1991)
c) attraction of allies and potential mates (Wrangham 1977; Mitani and Nishida 1993)
d) signalling food availability (Goodall 1986; Wrangham 1977)
e) expression of status (Clark and Wrangham 1994)

The idea that pant-hooting serves to inform others about food availability was based in the fact that males were more likely to give *pant-hoots* when food was more abundant (Wrangham 1977), and individuals who gave food calls were joined more often than those who did not vocalize (Wrangham 1977; Ghiglieri 1984, Kibale). However, another study in Kibale did not support the last claim (Clark 1991).

Although some of the hypotheses listed above are difficult to investigate in captivity, the proposed function of food-associated calls as indicating food availability can be studied by concentrating on the factors that may affect food calling, i.e. by manipulating in captivity the quantity, quality or divisibility of the food. Previous research on chimpanzees' food calls in captivity has demonstrated that the probability of producing a food call is related to the quantity and divisibility of the food discovered. Hauser and Wrangham (1987) conducted experiments on food calls with captive chimpanzees, manipulating different quantities of food (5, 10 and 20 prunes). The results showed that chimpanzees finding a preferred food item do not always call (there were no calls when the chimpanzees found 5 prunes), and that larger food piles are more likely to elicit calls (*rough grunts*) than smaller ones. A question that was not asked in this experiment is whether chimpanzees are more likely to call when they find food that can be easily shared with other group members (divisible food) than when they find food that cannot be shared (non-divisible food). Hauser et al. (1993) conducted an experiment on this question with a group of four adult chimpanzees housed in Sacramento Zoo (California). They presented the chimpanzees with four different conditions of food: 5, 10, 20 small pieces of watermelon, or 1 large piece (non-divisible), equivalent in quantity to the 20 small pieces. In 19 of a total of 40 trials the discoverer called upon finding watermelon. Results showed that there was a significant effect of the amount and divisibility of food. When the chimpanzees found the 20 pieces of watermelon they called more than when they found 5, 10 pieces or a single large piece of watermelon. Moreover, one large piece elicited more calls than 5 but not 10 small pieces. Thus, large amounts of food were more likely to elicit calls than small amounts, and individuals called more to divisible food than to non-divisible food items. Two different call types were given: *pant hoots* and *rough grunts*. *Rough grunts* were always the first vocalization to be given. With only one exception, *pant-hoots* were always given by adult males when discovering large amounts of divisible food. This work has implications for both call referentiality and food sharing.

Food-associated calls have been described as representational or referential signals in several primate species (see this thesis' Introduction). The pattern of production of *rough grunts* and *pant-hoots* observed in the study above (Hauser et al. 1993) provided evidence on the issue of chimpanzees' food calls as referential signals. It suggested (following the model of referentiality proposed by Marler et al. 1992) that *rough grunts* provide the contextual referent whereas interlocked *pant-hoots* provide information to others about the caller's level of arousal in the context of food (Hauser et al. 1993).

De Waal (1989) found that captive chimpanzees readily share food. He described two types of sharing, i.e. passive relinquishment of food, where an individual removed some or all the food from the possessor's hands or mouth, in a relaxed manner, without any opposition from the possessor; and active sharing, where an individual split up a piece of

food and actively handed it over with his/her hand to a conspecific without any aggression or use of force in either side. Although passive sharing is common among chimpanzees, voluntary or active sharing is very rare (he observed only 5 cases, 0.2% of all food transfers). The apparent divisibility of the food found affects the sharing behaviour of individuals. In Hauser and Wrangham's (1987) study, passive sharing occurred in all cases when the animals had previously called. In Hauser's et al. (1993) study three cases of active sharing were observed, all when the discoverer split the large piece of watermelon. Seven cases of passive sharing occured, where the individual in possession of food allowed another to take some food away, with no consistent condition pattern.

There were several aspects in the two studies described above that needed further investigation. The first experiment that I will present in this chapter constitutes an attempt at doing so. The specific aims of this first experiment were the following:

i.) To replicate the Hauser et al. (1993) experiment with a larger group of chimpanzees in order to obtain more data on the food quantity and divisibility effects, and on the sharing behaviour of discoverers. Particular attention was given to observing if there were cases of active sharing, whether they occurred when the food was divisible or non-divisible, and if there was a consistency between food calling and sharing, i.e. whether an individual who had previously called would afterwards share the food with others.

ii.) To explore the hypothesis of the possible referentiality of the two different food-associated calls. It is important to know whether a call labelled as a 'food call' is communicating about food alone or is communicating about excitement level or the behaviour the caller is going to do next. So, in order to achieve this the design aimed to isolate the calls that occur in food contexts, to demonstrate that food calls are directly related to food and not part of a larger behavioural pattern.

In this thesis' Introduction I reviewed recent research indicating that animals modulate their production of food calls as a function of the presence or absence of particular individuals (reviewed in Marler, Karakashian and Gyger 1991). The most recent work about the audience effect on chimpanzees has been done by Mitani and Nishida (1993) with wild chimpanzees. They studied the effects of several social factors on *pant-hoot* production, showing that adult males called more frequently when alliance partners or associates were nearby, compared with when they were alone. The two highest ranking males and one middle ranking male called more frequently when estrous females were nearby than when they were absent. Three low ranking males called less often when estrous females were nearby. In their study they concluded that males may give *pant-hoots* to particular audiences within their social group, specifically to maintain contact with and

to recruit allies and associates. An important point that these authors highlighted is that evidence about the precise response of the receivers of the calls (e.g. approach or seek out their allies and associates) is needed to provide further support to these claims. However, experimental work on the audience effect has never been done in chimpanzees because the conditions in the wild do not allow researchers to manipulate the composition of social audiences. This issue can be investigated in captivity by manipulating the social audience that will hear the calls to see whether chimpanzees modify their amount of calling depending on which individuals are present, and by recording all behavioural responses of receivers. Thus, the second experiment that I present in this chapter represents an attempt to create a situation in which one can determine if chimpanzees take into account their social audience when they give food-associated calls. The specific aims of the experiment were:

iii.) To find out under what social circumstances discoverers of food signal their discoveries or suppress a signal, creating as many combinations of different social audiences as possible, i.e. a high-ranking male alone or with others; a low ranking male alone or with others.

iv.) To collect further data on the effect that divisible versus less divisible food has on calling behaviour, on the effect of the presence of estrous females on males' calling and sharing behaviour, and on the specific responses of receivers of the calls in each social context tested.

Finally, if animals can control voluntarily the production of food calls depending on the social context they are in, then they may be able to emit or withhold these calls according to the specific gains either behaviour confers them at the time, allowing for the manipulation of information and the emergence of deception. Thus, a last aim of the experiment was:

v.) To create a situation under controlled conditions in which possible cases of deception by withholding information (suppressing a call) or even falsifying information may take place. The costs and benefits associated with the failure to signal, and the possibility that individuals may expect to obtain information from other group members in certain contexts will be explored.

10.2. GENERAL METHODS

Subjects and group composition

A group of 12 captive chimpanzees (*Pan troglodytes*) was observed at Edinburgh Zoo, Scotland from March to August 1993. The group consisted of five adult males, four adult females and three infants (see Table 10.1. for group composition, age and origin of individuals). All adult individuals were unrelated except an adult male and an adult female whose mother was the oldest female in the group. Only adult individuals were used for collection of behavioural and vocal data during the experiments.

Over the past this group of chimpanzees has been the subject of different behavioural and enrichment projects, i.e. Stephen Myles (1993), St Andrews University, 'the use of tools to crack nuts'; Iddo Oberski (1992), Stirling University, 'long term study on grooming reciprocity'. Records of births, matings and females' estrous cycles have been kept by the personnel of the Zoo continuously since the colony was established.

Description of enclosure and feeding routine

The enclosure where the chimpanzees were housed was divided into a large outdoor area (20 x 10 x 6m) connected to an indoor series of cages by a tunnel. This tunnel was open 24 hours a day, so the animals could move freely along the different cages, or even hide themselves from the public view. However, they could not see what was happening in the outdoor area from this tunnel. The outdoor area (see plate 9) included several metal structures forming a resting platform, and three artificial nests, together with mobile tree trunks, hanging tyres, a large mesh made of ropes, and an artificial termite mound which was never filled with food when an experiment was going to be conducted. The vegetation was relatively dense. The chimpanzees were locked in the indoor compartment once a day for about 20 minutes, during which the keepers cleaned the outside area. From the indoor cages they could see part of the outdoor enclosure through two big windows.

In the wild, chimpanzees feed on a large variety of foods, ripe fruit being one of the main components of their diet. They spend a large amout of time travelling and foraging for the ripest food sources. The diet of the chimpanzees in this zoo was very varied, including fruits, seeds, nuts, vegetables and horse meat. The chimpanzees had a complex daily feeding routine, i.e. four supplies of food scattered in the enclosure at different times of day, in an attempt to simulate their feeding and foraging habits in the wild.

Table 10.1. Group composition, age and origin of chimpanzees at Edinburgh Zoo (1993)

Name	Sex/Approximate age	Origin
Ricky	Male/ 31	Wild born
Leo	Male/27	Wild born
David	Male/18	Captive born
Louis	Male/16	Wild born
Tom	Male/15	Captive born (Cindy)
Cindy (+infant)	Female/28	Wild born
Lucy	Female/17	Captive born
Emma (+infant)	Female/12	Captive born
Lindsey (+infant)	Female/10	Captive born (Cindy)

Legends of symbols
: exit doors through which the chimpan came out.
: places where the food was hidden

Plate 9. View of the outdoor area where chimpanzees are housed in Edinburgh Zoo, Scotland with exit doors and hiding places marked with symbol

These four supplies were distributed as follows: a small provisioning was given at 9.00am to lock the chimpanzees in the indoor compartment, followed by another small provisioning at 11.00am scattered in the outdoor area before the chimpanzees were released. Then, the biggest feeding of the day took place at 12.15pm, when the educational department of the zoo gave a talk about the chimpanzees, and a final provisioning occurred between 5.00-5.30pm.

10.3. EXPERIMENT 1: Effect of food quantity and divisibility on calling behaviour

10.3.1. Methods: experiment 1.

This experiment had basically the same design as the one conducted by Hauser et al. (1993) in the Sacramento Zoo, California with the exception of the differences in the daily feeding routine of the chimpanzees in the two zoos, and one of the stimulus' condition used.

Stimulus used

The stimulus used in the experiment was watermelon. Watermelon is not part of the chimpanzee's regular diet in Edinburgh zoo, but the keepers had confirmed that on the rare occasions when they had fed the animals watermelon it was a highly preferred food item. A further reason for using this fruit was that it can be split into pieces, allowing presentation in different quantities, but it can also be used in a non-divisible form, by presenting a whole watermelon. Moreover, its bright colour makes it salient, hard to go unnoticed while foraging. Watermelon was presented in four different conditions: 5, 10, 20 pieces or a whole watermelon, equivalent in quantity to the 20 pieces. Each piece of watermelon was approximately the same size (6x6cm), and all pieces were placed in a pile upon presentation.

Protocol

Trials were conducted from April to August 1993. A total of 20 trials were conducted, five for each of the four conditions of food presented. A maximum of two trials was conducted each week. Trials began between 10.30-12.00am, except two (9-6-93; 6-7-93) which were conducted before the afternoon feeding, at 15.45 and 14.15pm respectively. The reason why I had to conduct these two trials in the afternoon was that the

chimpanzees could not be locked inside in the morning (11.00am). A very common problem I had in this zoo was the impossibility of locking the chimpanzees in the indoor compartment because some individual would not want to come in (specially during periods of high levels of tension between the males, caused mainly by the fact that one of the females was in estrous).

In order to clean the outside area, the keeper locked the chimpanzees between 9-10am in the indoor cages, feeding them a small amount of food. Before releasing the chimpanzees, the keeper scattered around some food in the outdoor enclosure. Thus, the chimpanzees were used to foraging in the outdoor enclosure immediately upon being released. The day I was going to conduct a trial, I told the keeper in advance so he would not scatter food in the outdoor area. While he cleaned the outdoor area, I placed blinds (a pair of sheets) in the windows of the indoor cages, to avoid the chimpanzees seeing what was happening in the outdoor area (blinds were also placed in days when no trial was conducted, in order to avoid the animals associating the blind with the placement of watermelon). Before releasing the chimpanzees, I concealed watermelon outside in one of the food conditions described, in one of several different places: under the vegetation, a wood trunk, inside a tyre, or high up in one of the nests (see plate 9, for hiding places). The order of presentation of each condition was randomized. Once the watermelon was concealed, the chimpanzees were released. The trial started as soon as the first chimpanzee came out from one of the exit doors (see plate 9). The trial was videotaped with a S-VHS Panasonic MS2 camera placed in a tripod, pointed towards the place where the food was hidden. I left the camera filming the discovery moment, while I recorded behavioural data and vocalizations onto a Marantz PMD-430 stereo cassette recorder, a clip microphone (Beyer MCE6) and a Sennheiser directional microphone ME88 with wind screen. After the discovery moment I stopped the camara and concentrated in describing any interaction or calling between the discoverer and other individuals. Observations continued for a period between 5-30 minutes (mean=8 min.) after the last piece of watermelon had been eaten, depending on whether or not the chimpanzees moved out of sight into the indoor enclosure.

Data collected during trials

Before the chimpanzees were released, I marked in a map of the enclosure the location where the food was hidden. After the trial had finished, I marked the spatial location of individuals as they came out and at the time when the food was discovered. The following information was recorded in each trial:

a) at what time were the chimpanzees released?
b) which individuals came out first?

c) at what time they discovered the food?
d) information about the discoverer:
- who discovered the food?
- did it call upon seeing the food?
- which calls did it give and how many?
- how many pieces did it get?
- did it share the food with other individuals (active sharing/ passive relinquishment)?
e) what was the approximate distance of the individual nearest to the discoverer?
f) response of the listeners of the call:
- did they call as well?
- did they approach the discoverer?
- did they grab some food?
- did they supplant the discoverer (an individual approached to within one meter of the discoverer and the discoverer moved from the spot, abandoning whatever food was left)?
- did they charge or launch an aggressive display against the discoverer?
g) were there any females in estrous?

To analyse the results I concentrated on the transcriptions of the video tapes and on the audio tape information. Statistical analyses focused on the calling and sharing behaviour of discoverers, and on the responses of hearers of the calls. ANOVA and t-tests were used when data were normally distributed and had homogeneous variances, otherwise non-parametric statistics were applied.

10.3.2. Results: experiment 1.

Most chimpanzees in the group discovered the food at least once, except two individuals: an adult female, Cindy, who rarely spent time in the outdoor enclosure and therefore had little opportunity of finding it, and an adult low-ranking male, Tom, who I never saw foraging very actively in the outdoor enclosure even when the keepers had scattered food around. In 20 trials, females discovered the food on 10 occasions and males on 10. In seven trials (35%) the individual who came out first was also the one who found the food. In order to find out if individuals who came out first discovered the food in more trials than individuals who did not come out first a Fisher Exact Probability test was used. The probability of finding the food was not affected by the fact of being or not the first one to come out (David, $p=0.71$; Lindsey, $p=0.9$; Louis, $p=0.8$; Lucy, $p=1$; Ricky, $p=1$; Leo, $p=0.39$; Emma, $p=0.21$).

The time taken to discover the food from the moment the first chimpanzee came out to the outdoor enclosure varied between 0.37-7.6 min. (mean=1.8 min.; SD=1.7; n=20)(see table 10.2.). Considering at random a number of trials conducted at the beginning and at the end of the study, the time elapsed for the first five trials was not significantly different from the time elapsed for the last five (t=1.01; df=4; p=0.37), showing no effect of habituation to the procedure (see also figure 10.1.).

Plates 10, 11 and 12 present an example of three different moments during one experiment (20-8-93) in which a female, Emma, found 20 pieces of watermelon hidden inside a wood trunk.

Calling behaviour

In 14 trials (70%), the discoverer called upon finding watermelon. In order to test if there was any effect of the condition in which the food was presented (5, 10, 20 pieces or a whole watermelon) in the calling behaviour of discoverers, a one-way ANOVA using the number of calls per discoverer in each condition was perfomed (see table 10.2.). There was no significant condition effect in the calling behaviour of individuals (F=0.27; df=3;19; p=0.845).

Four different call types were given: *rough grunts*, *pant-hoots*, *screams* and *squeaks* (see Table 10.2.). *Rough grunts* were the most common vocalization and always the first one to be given when other calls were produced. While *rough grunts* were given in all conditions, *pant-hoots* were only given in one trial by a high-ranking male, when he discovered 20 pieces of watermelon. An ANOVA using the number of *rough grunts* per condition, did not show a significant condition effect (F=0.50; df=3;19; p=0.686). A Kruskal-Wallis one-way analysis of variance (since these calls were not normally distributed) revealed no condition effect on the number of other types of call (*screams*, *squeaks* and *pant-hoots*)(H=6.82; df=3; p=0.079; adjusted for ties).

Although there might be different costs and benefits associated with calling for a male or female chimpanzee when finding food, males did not give significantly more calls than females upon finding the watermelon (t-test on mean number of calls per each male and female that discovered the food; t=1.5; df=4; p=0.21). There was also no significant difference in the number of *rough grunts* given by males and females (t-test on mean number of rough grunts per each female and male; t=1.18; df=14; p=0.26). The rank of the male discovering the food had equally little effect. High-ranking males did not call more than low-ranking ones (t-test on number of calls given by high-ranking versus low-ranking males; t=2.24; df=2; p=0.15).

Table 10.2. Experiment 1. Results on calling behaviour

Condition	Date	Discoverer	Approximate time to discovery (min)	Number of calls given by discoverer	Pieces eaten by discoverer**	Proximity of nearest indiv. (m)	Females in estrous
	5/5/93	EMMA	2.00	6	5	0.5	No
	9/6/93	LINDSEY	2.40	5	2	0.5	Yes
5 pieces	16/6/93	DAVID	1.00	5	2	1	Yes
	22/6/93	EMMA	0.54	0	5	3	No
	25/8/93	RICKY	1.40	0	3	1	No
	13/5/93	RICKY	1.00	4	9	2	Yes
	20/5/93	LEO	1.00	14	3	1	Yes
10 pieces	26/5/93	LUCY	2.00	5	6	2	No
	23/6/93	EMMA	1.40	0	5	5	No
	29/6/93	RICKY	1.00	3	5	4	No
	19/5/93	LEO	1.00	11	5	3	Yes
	2/6/93	EMMA	0.50	2	11	5	Yes
20 pieces	6/7/93	EMMA	7.64	0	9	6	No
	18/8/93	RICKY	1.00	5	10	4	No
	20/8/93	EMMA	2.00	0	10	2	No
	27/5/93	LOUIS	5.00	8	5	4	No
	11/6/93	EMMA	0.48	2	17	4	Yes
1 WM	11/6/93	LOUIS	3.30	2	0	5	Yes
	30/6/93	LINDSEY	0.37	0	5	4	No
	24/8/93	RICKY	1.40	4	11	2	No

* According to Marler and Tenaza's (1977) catalogue of chimpanzees' vocalizations.

** If the condition was a whole watermelon, I estimated how many pieces the discoverer ate by spliting it.

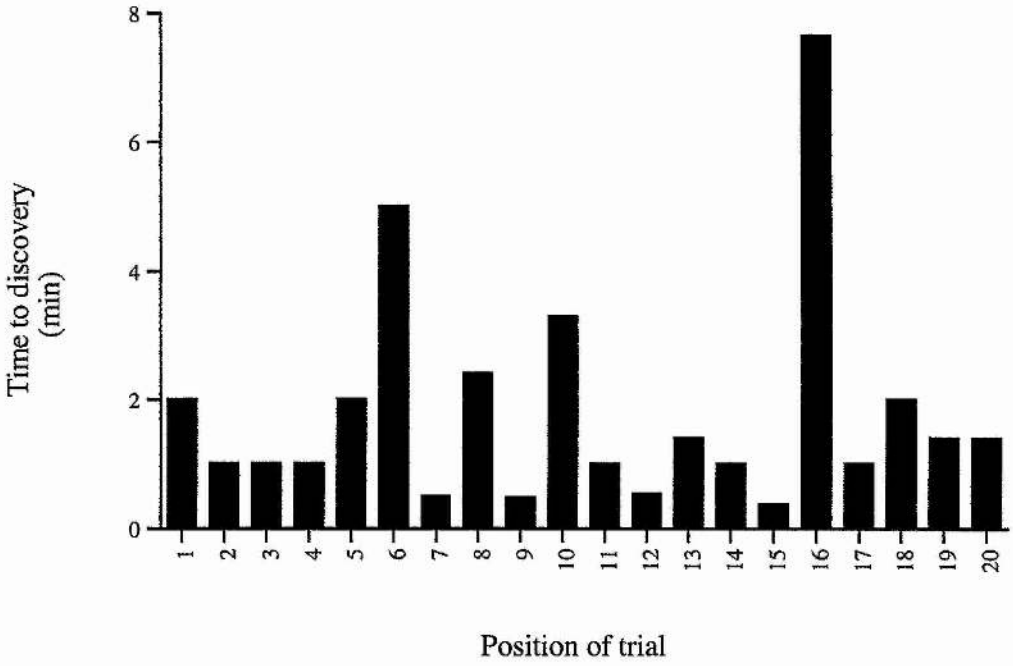

Figure 10.1. Time to discovery (min) in each trial

Plate 10, 11 and 12. Three different moments in the experiment of the date 20-8-93. Time: 11.30am. An adult female, Emma, discovered 20 pieces of watermelon hidden inside a wood trunk and did not give any calls or share the food with others.

Plate 10. Moment 1. Two minutes after the first chimpanzee came out (Leo), Emma discovered the food. In the photograph, Emma (female with the infant) was walking past the wood trunk, saw the food inside and started grabbing pieces without calling. Lindsey (female behind her) saw her from the distance and approached her silently. The male on the left had not seen the food nor the females eating because the wood trunk prevented him from seeing them. The video camera was filming the discovery moment.

Plate 11. Moment 2. The discoverer, Emma, had pulled the food outside of the trunk and Lindsey, on the right, was looking inside and trying to get some pieces. No other group member had seen the food yet.

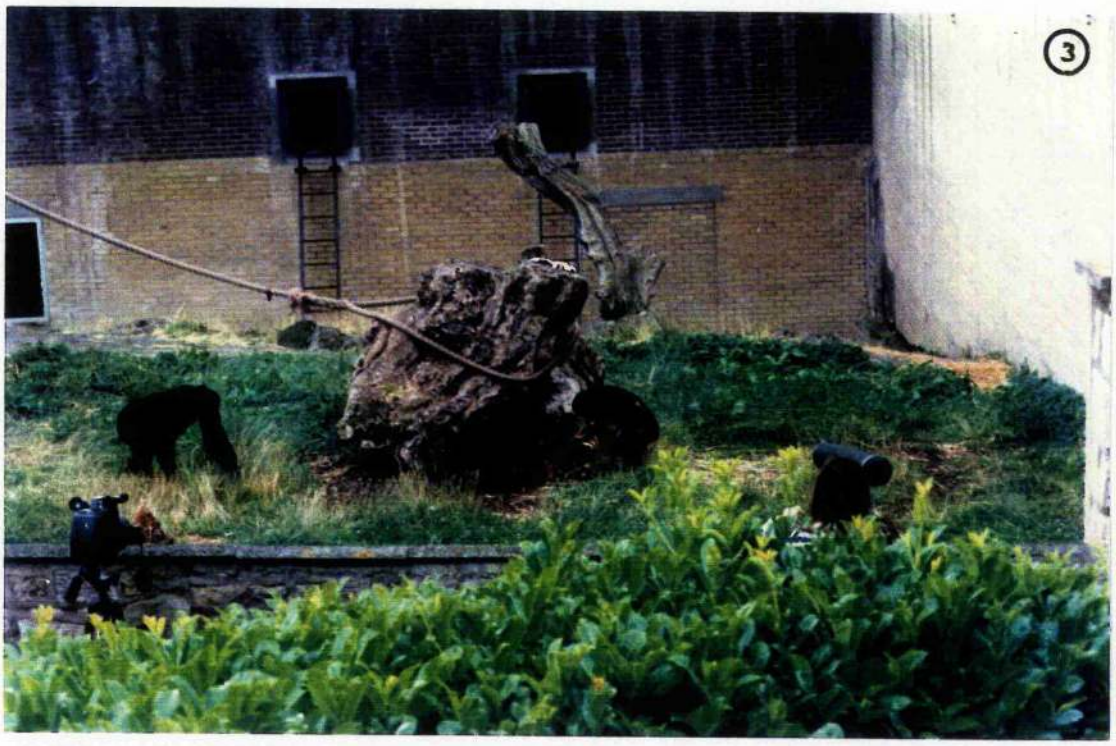

Plate 12. Moment 3. A minute later, two of the males, David and Tom, saw the females eating and approached them. David, a high-ranking male (on Emma's left side), was grabing some pieces, and Tom was approaching. One of the male gave soft rough grunts as he was eating. Lindsey walked away with five pieces of watermelon as soons as the males arrived. Emma, grabbed as many pieces as she could carry (nine pieces) and moved away with the food. The experimenter was standing on the right with a gun microphone, recording the calls and describing the behaviour of the chimpanzees.

The effect of the rank of the female discovering the food could not be investigated because the female hierarchy at the time the study was conducted was not clearly established.

If calling usually attracts other conspecifics to the food source, it can then be expected that the discoverer may risk increasing feeding competition and losing some of the food by announcing its discovery. However, whether the discoverer called or not upon finding the watermelon did not affect the amount of food eaten (t-test on pieces eaten by discoverer when it called versus when it did not call; t=0.37; df=10; p=0.72)(see table 10.2.). Nor did the proximity of other individuals to the discoverer affect its decision to call or not. The proximity of the nearest individual in the discovery moment was divided into three categories, very close (0.5-2m), near (3-4m) and far (5-6m). A Kruskall-Wallis test was used on the number of calls given by the discoverer in these three categories, finding no effect (H=5.35; df=2; p=0.07; adjusted for ties).

One of the hypothesized functions of chimpanzees' calling when finding food is that it attracts potential reproductive partners. In a total of 10 trials in which males discovered the food, a female (Lucy) was in estrous in five trials (see table 10.2.). However, males did not call more in trials in which a female was in estrous in the group than in those in which there was no female in estrous (Fisher Exact probability test; p=0.5).

Food sharing behaviour

Nine cases of food sharing by the discoverer were observed. Six of these were cases of passive relinquishment of food (de Waal 1989) and three were active sharing (see Introduction). All cases of active sharing occurred when discoverers found a whole watermelon and split it into smaller pieces, handing them over to another individual; there was no consistent pattern for passive relinquishment (see Table 10.3.). In all cases in which sharing occurred, the discoverer shared the food with females. Only in two trials did the discoverer share the food with a male as well as with a female.

Taking all the cases of sharing (active and passive) together, the Fisher Exact Probability Test revealed that there was a significant difference in the amount of sharing between divisible (five, 10 and 20 pieces together) and non-divisible foods (one watermelon). More sharing occurred when individuals found non-divisible food than when they found divisible food (Fisher Exact test; p=0.01).

Table 10.3. Experiment 1. Food sharing behaviour and responses of other individuals

Condition	Discoverer	Number of calls	Sharing	Response of receivers	Females in estrous	Proximity of nearest indiv. (m)
5 pieces	EMMA	6	No	Approach, display	No	0.5
	LINDSEY	5	No	Approach, call, supplant	Yes	0.5
	DAVID	5	No	Approach, call, grab food	Yes	1
	EMMA	0	Yes (passive)	Approach, display	No	3
	RICKY	0	Yes (passive)	Approach, grab food, call, supplant	No	1
10 pieces	RICKY	4	No	Approach, call, grab food	Yes	2
	LEO	14	Yes (passive)	Approach, call, grab food	Yes	1
	LUCY	5	No	Approach, call, grab food	No	2
	EMMA	0	No	Approach, call, grab food	No	5
	RICKY	3	Yes (passive)	Approach, call, grab food	No	4
20 pieces	LEO	11	No	Approach, call, grab food	Yes	3
	EMMA	2	No	_	Yes	5
	EMMA	0	No	_	No	6
	RICKY	5	No	Approach, call, grab food	No	4
	EMMA	0	No	_	No	2
1 WM	LOUIS	8	Yes (active)	Approach,call, display	No	4
	EMMA	2	Yes (passive)	Approach, call	Yes	4
	LOUIS	2	Yes (active)	Approach, aggressive display, threat	Yes	5
	LINDSEY	0	Yes *	Approach, call	No	4
	RICKY	4	Yes (act.&pas)	Approach, call, display	No	2

* In this trial the discoverer, Lindsey, went inside with the whole watermelon and I coud not see the way she shared it (active or passive sharing). One of the other females had 3/4 of it though.

In order to investigate whether there was any relation between calling and sharing, for instance if an individual who had previously called would share afterwards, the Fisher Exact Probability Test was used. Individuals who had called upon discovering food showed no significant difference in the amount of sharing when compared to individuals who had not called upon discovering food (Fisher Exact test; p=0.35). Thus, there does not seem to be any relation between calling and willingness to share.

Male chimpanzees may gain more than females if they share the food, specially if there is a female in estrous with whom they could mate in the future. However, no difference was found in the amount of sharing of males and females (Fisher Exact test, p=0.15), or in the amount of sharing when there was an estrous female in the group versus when there was not any (Fisher Exact test, p=0.30)(see table 10.3.).

The decision to share or not share may have been influenced by the proximity of the nearest individual to the discoverer (ranged from 0.5-6m). However, there was no difference in the proximity of the nearest individual in trials when the discoverer shared versus trials when it did not share (t-test; t=0.39; p=0.70; df=17).

In five of the six cases in which a male was the discoverer and sharing took place, he shared the food with Lucy, who was in estrous in three of the trials. Two of these were cases of active sharing, in which the male shared the whole watermelon with Lucy. Since active sharing is a rare behaviour among chimpanzees, I think it is worth describing how these cases of active sharing took place and find out if they have anything in common. I present below a description of these two instances of active sharing with Lucy and a third one in which a male shared the food with a different female, Emma.

SEQUENCE 1 (transcribed from video)

Date: 27-May-1993. Time:11.48am. Condition: a whole watermelon. No females in estrous.

"Louis was sitting in the highest pole of the enclosure (a big wooden tree, 10 meters from the ground), right at the top, eating a whole watermelon he had found. Lucy had followed him to the top and was getting closer to him. Once she reached him, he bit off a piece of watermelon and handed it over to her. Ten seconds later, before Lucy had made any further approach he handed over to her another piece of watermelon. She finished eating both pieces and looked up towards him. He continued eating. Lucy stretched out a hand towards the food but Louis avoided her arm, moved the watermelon higher, bit off another piece and handed it to her. Twenty seconds later, Lucy grabbed from Louis' hands four other pieces of watermelon without any resistance on his side. He passively allowed her to take this food. Lucy grabbed the biggest piece from his mouth and climbed down with it, while the others foraged below the place where Louis had been eating".

SEQUENCE 2 (transcribed from video)

Date: 11-June-1993. Time:11.46am. Condition: a whole watermelon. Lucy in estrous.

"Louis, a low-ranking male, found a whole watermelon and climbed up the highest pole in the enclosure with it. Leo and David, the two high-ranking males in the group, followed him. Leo started barking and displaying towards Louis, 4 meters away from him. David joined Leo and both started pant-barking, jumping up and down the ground, and screaming towards Louis. Louis was standing in the top of the pole with the watermelon in one hand, head-bobbing and fear grimacing towards the two males. Lucy climbed up towards Louis, who was holding the watermelon in Leo's direction (4 meters away). As she reached him, he offered the whole watermelon to her. She grabbed it, climbed down with it and moved towards one of the artificial nests. Leo and David stopped threatening Louis and followed Lucy closely".

SEQUENCE 3 (transcribed from video)

Date: 24-August-1993. Time:11.47am. Condition: a whole watermelon. No females in estrous.

"Ricky, a low-ranking male, had found a whole watermelon and was sitting in the metal structure surrounded by other chimpanzees (Lindsey, David, Louis, Lucy). He had already shared some pieces of watermelon with David and Lucy, allowing them to take some pieces away from him. However, they kept insisting in their begging. Suddenly, Leo and David started pant-hooting and displaying. David launched a charge towards Emma and she moved away quickly, screaming and fear grimacing, walking towards Ricky. Ricky continued eating but moved away a few meters from David. He then looked at Emma who was approaching him, still screaming and held out a piece of watermelon towards her. She immediately stopped screaming, grabbed the piece and sat next to Ricky chewing the watermelon".

When looking at these three sequences in which a male actively shared the food with a female, it can be seen that two of them have in common that there was tension in the group because two high-ranking males were performing aggressive displays towards the possessor of the food. Thus, the active sharing performed by the male, by handing a large portion of the whole watermelon to a female may have been a way of reducing tension between the males, specially since the males stopped displaying immediately after the food was handed over to the female.

Responses of other individuals

The responses of other individuals after the discoverer had found the food were varied: they approached the discoverer in 85% of the trials, called in 70%, grabbed some food in 45%, behaved aggressively towards the discoverer in 20% and supplanted it in 10% of the trials (see table 10.3.). In order to test if any of these responses were affected

by whether the discoverer had given a call or not when finding the food, the Fisher Exact Probability test was used. There were no significant differences in any of the responses in trials when the discoverer had called versus those in which it had not called (approach discoverer, p=0.18; call, p=0.18; grab food, p=0.32; supplant discoverer, p=0.44; aggressive display, p=0.45). Furthermore, it may be expected that discoverers who shared the food with others received less aggression or were supplanted in fewer occasions than discoverers which did not share. However, no difference was found in the number of aggressive displays or supplants received by discoverers who shared the food versus those which did not (Fisher Exact, aggressive displays, p=0.08; supplants, p=0.52)(see table 10.3.). As a result of aggressive displays the discoverer lost food in 3 of the 5 trials concerned (all food in one trial). There was also only one case in which a discoverer (a low-ranking male) was vocally threatened and aggressively charged by a coalition formed by two high-ranking males. He lost all of the food (a whole water melon)(11-6-93).

10.3.3. Discussion: experiment 1.

Unlike the findings of previous researchers (Hauser and Wrangham 1987; Hauser et al. 1993), this experiment's results showed that chimpanzees in Edinburgh zoo did not modify their calling depending on the quantity or divisibility of the food they discovered. There are two possible answers to the question of why did this study not show the effects of overall food quantity and divisibility found in the Hauser et al. (1993) experiment. One is that because of the particular feeding routine in Edinburgh zoo (four or even five provisionings per day), these chimpanzees were simply not hungry and/or motivated enough by the food during the experiments. In some of the trials, the chimpanzees still had food in the indoor cages when they were released to the outdoor compartment. However, this might not have been an important factor in explaining the difference from Hauser's work, because in my experiment the chimpanzees called in 14 of 20 trials (70%), whereas in the Hauser et al. experiment they called in 19 of 40 trials (48%). Thus, although the hunger level factor was controlled better in the Hauser et al. experiment, the Edinburgh chimpanzees still called a greater percentage of the times. The second possible answer is that the size of the group and the size of the enclosure they were housed in were very different. In the Sacramento zoo a group of four adult chimpanzees found the food in a small outdoor enclosure, and therefore the possibilities of being caught with food without having previously called were higher than in Edinburgh. Moreover, the opportunities to escape in case of an aggressive reaction by any of the other individuals were scarce. By contrast, in Edinburgh zoo a larger and more complex social group with

several infants found the food in a spacious outdoor area with a better chance to get away in case of necessity.

However, my results confirmed the existing idea in the literature that the apparent divisibility of the food found affects the sharing behaviour of chimpanzees. Discoverers shared more (both active and passively) when they found non-divisible food than when they found divisible food. Moreover, active sharing occurred only when the individual found a non-divisible watermelon, split it and handed over a piece to another chimpanzee (as in Hauser et al. 1993). Both facts suggest that in chimpanzees' sharing behaviour, an individual's decision to share with others may be guided by the perceived divisibility of the food item. But, why should a chimpanzee share more when finding non-divisible foods than divisible ones? De Waal (1989) found that sharing among adult chimpanzees can be easily induced with a concentrated, harder to divide food source (e.g. a bundle of branches of a preferred tree species tied together). It is possible that when a male chimpanzee for example finds a pile of 10 or 20 pieces of fruit, he may get some pieces for himself without sharing any of the food, since there will be some left for others, while when he finds a whole watermelon it is more difficult to eat it all at once without sharing with others, and he might be forced to share it in order to avoid arising any tension.

A different result related to the second objective mentioned in the Introduction is that four types of call occured in the experiment, *rough grunts*, *screams*, *squeaks* and *pant-hoots*. Interestingly, as in the experiments conducted by Hauser and Wrangham (1987) and Hauser et al. (1993), *rough grunts* were the first vocalization to be given, and the most common one (by both sexes). *Pant-hoots* however, were not as common as in Hauser et al. experiment, but, as in their study, were given mostly by males upon finding the largest pile of food (20 pieces). *Screams* and *squeaks* were also predominantly given upon finding large amounts of food (10 or 20 pieces).

In a social situation in which the whole group is present when an individual discovers a preferred food, chimpanzees may not alter their calling behaviour. However, I wanted to test if chimpanzees would alter or supress their calling if only particular individuals were nearby or if they were completely on their own. For this reason I decided to carry out the experiment presented in the following section, already outlined in 10.1.

10.4. EXPERIMENT 2: The social audience effect on food calling behaviour

10.4.1. Methods: experiment 2.

Because of the difficulties encountered in the previous experiment when locking the chimpanzees in the indoor compartment, I decided to try a more opportunistic approach, for which there was no need to lock up the chimpanzees or interfere in any way in their daily routine. The aim was to investigate the effect that different social contexts or audiences may have on the decision to give or withhold a food call. This sort of approach consists in creating a situation in the everyday life of the chimpanzees in which behaviours that occur rarely may come out (e.g. cases of sharing or deception by witholding information) and can be studied under controlled conditions. Furthermore, I wanted to obtain more data on the effect of divisible versus non-divisible foods on the food calling behaviour of these chimpanzees.

Stimulus used

As in the previous experiment, the stimulus used was watermelon, in two different forms, 20 pieces or a whole watermelon equivalent in quantity to the 20 pieces (non-divisible food item). The order in which I conducted a trial with either condition was randomized.

Assessment of rank to males

To establish the approximate rank of the chimpanzees in this group, I used the existing data in the zoo about the group's social structure provided by previous researchers such as Iddo Oberski who studied grooming reciprocity in the group. Although the dominance hierarchy in a captive group of chimpanzees may vary over short periods of time depending on a number of factors, e.g. the number of female allies that a male can count on (de Waal 1982), the male hierarchy in this group at the time the study was conducted consisted of two high ranking males (David and Leo) and three low ranking ones (Louis, Ricky and Tom).

Protocol

Opportunistic trials were conducted from May to July 1993. A total of 21 trials were conducted, nine with the whole watermelon and 12 with the 20 pieces. Of these 21 trials 15 were conducted in the afternoon, just before the chimpanzees had their last feeding, and six were conducted in the morning, after their two small feedings. There were only

four days in which both types of experiments were conducted, experiment 1 in the morning and experiment 2 in the afternoon.

By the time I started this experiment, the chimpanzees were already used to seeing me behind a wall where the public could not go (see plate 13). By observing them from this wall I realized that it was often the case that for long periods of time only two or three individuals were spending time resting, foraging or grooming each other in the outdoor area on their own, while the rest of the group was in the indoor cages (two doors were always open so the animals could go in and out at wish). Although in some places of the outdoor area the chimpanzees could be seen from the indoor cages by other individuals through the two big windows, this was not possible if they were in an area below a small hill, closest to the wall on which I was positioned. Thus, either in the morning or in the afternoon, I would wait in the wall where I usually stood, until a male alone or accompanied by another individual were solitary in the outdoor enclosure. The design of the experiment aimed to test six possible social audiences: a high or low ranking male alone; a high or low ranking male with a conspecific of the same sex; a high or low ranking male with a conspecific of the opposite sex (see table 10.4.). Once one of these social audiences happened to be in the outdoor enclosure on their own, I placed the video camera in a tripod, ready to start filming, and waited for the right conditions to begin a trial. The conditions that had to be met before starting a trial were the following:

a. the individuals selected as targets (i.e. one male of a given rank alone, or the same male with either another male or an adult female) had to be out of sight from the rest of the group, positioned in the above mentioned area which could not be seen from the indoor cages
b. only adult males who had not discovered the food that same day in experiment 1 were selected as targets (only in one occasion the same individual who discovered the food in the morning in experiment 1 was selected as target in the afternoon for experiment 2 because of a researcher's mistake).

Once these conditions had been met, I turned on the video camera, pointing it towards the target, and threw the watermelon over the wall 3-5 meters away from him, in one of two forms (20 pieces or a whole one) above mentioned (I always brought the watermelon hidden in a bag, out of sight of the chimpanzees). The calls given by the target and the other individual accompanying him ('second target'), and all the interactions occurring outside the camera's range once the watermelon was thrown, were described in a tape recorder.

Plate 13. Position from which recordings were made and the watermelon was thrown.

Table 10.4. Experiment 2: Number of trials conducted with different social audiences in the two food conditions, divisible versus non-divisible

	Male Alone		Male with same sex companion		Male with opposite sex companion	
	High-ranking male alone	Low-ranking male alone	High-ranking male+male	Low-ranking male+male	High-ranking male+female	Low-ranking male+female
Condition 1WM	2	2	–	3	–	2
Condition 20 pieces	3	1	2	4	1	1

As in experiment 1, observations continued for a period between 5-30 minutes (mean=8 min.) after the last piece of watermelon had been eaten, depending on when the target chimpanzees went to the indoor part of the enclosure. Table 10.4. presents a summary of the different social audiences with whom trials were conducted in each food condition.

Data collected during experiments

a) Information about the target:

- who was the target?
- were was it positioned?
- did it call upon seeing the food?
- which calls did it give and how many?
- how many pieces did it get?
- did it share the food with other individuals (active sharing/ passive relinquishment)?

b) Response of the second target (individual accompanying the main target):

- did it call as well?
- did it grab some food?
- did it act submissively (presented, fear grimaced, begged for food)?
- did it act aggressively (supplanted or displayed against the target)?

c) Response of the listeners of the call (individuals that heard the call from the inside or happened to come out at the moment the target was eating the food):

- did they call as well ?
- did they approach the target?
- did they grab some food?
- did they supplant the target?
- did they charge or launch an aggressive display against the discoverer?

d) Were there any females in estrous?

As in the previous experiment, for the analysis of results I focussed on the transcriptions of the video tapes and on the audio tape descriptions. Statistical analyses concentrated on the calling and sharing behaviour of the target, and on the responses of the second target and hearers of the calls.

10.4.2. Results: experiment 2.

Two of the six social audiences (high-ranking male with another male; high-ranking male with a female) could not be tested with the whole watermelon condition because no opportunities presented to conduct a trial when these audiences were alone in the outdoor enclosure.

Calling behaviour

All five males in the group were targets in at least one trial. In 11 trials (52%), the target called upon seeing the watermelon. Table 10.5. shows a summary of the total number of calls given by targets in each social context for which enough data were collected when seeing divisible (20 pieces) or non-divisible food (whole watermelon). In order to investigate both the food divisibility effect and the effect of social audience on the vocal behaviour of the target, given the small number of data in each social context, I ignored the rank variable and pooled the data of trials in which a male was alone or with other individuals (either another male or a female). I then used non-parametric statistics because the data were not normally distributed. To test if there was any effect of food condition or social audience in calling behaviour, a Kruskall-Wallis test with four levels was performed. It revealed that there were no significant differences between conditions in the number of calls given by the target when he was alone or with others ($H=7.36$; $df=3$; $p=0.062$; adjusted for ties). Since there was no effect of the two factors taken together I analyzed the effect of the two factors (divisibility of food and social audience) separately. A Mann-Whitney test on the number of calls given in the two food conditions, ignoring the social audience factor, showed that the target called more when he was presented with the divisible food (20 pieces of watermelon) than the non-divisible food (a whole watermelon)($W=160.0$; $p=0.035$, adjusted for ties)(see figure 10.2.). However, a Mann-Whitney test on the number of calls given by the target when alone or with others, ignoring the two food conditions, showed no significant difference ($W=76.0$; $p=0.3776$, adjusted for ties). I then used the Fisher Exact Probability test on the number of trials in which calling occurred in the two food conditions and two social audiences (alone/with other). When a male saw 20 pieces of watermelon, he did not call more in trials in which he was alone or with others (Fisher Exact test, $p=0.5$). Neither did a male who saw a whole watermelon call more in trials in which he was alone or with others ($p=0.27$). Moreover, the number of trials in which a male alone called or not when seeing 20 pieces or one watermelon did not differ ($p=1$), nor did the number of trials in which a male with other individual called or not upon seeing the two foods ($p=0.21$).

Table 10.5. Experiment 2. Total number of calls given by the target (pooled data)

	H-R Alone	L-R Alone	H-R+other	L-R+other
1WM	0 n=2	0 n=2	-	6 n=5
20 pieces	18 n=3	2 n=1	17 n=3	21 n=5

n= number of trials conducted

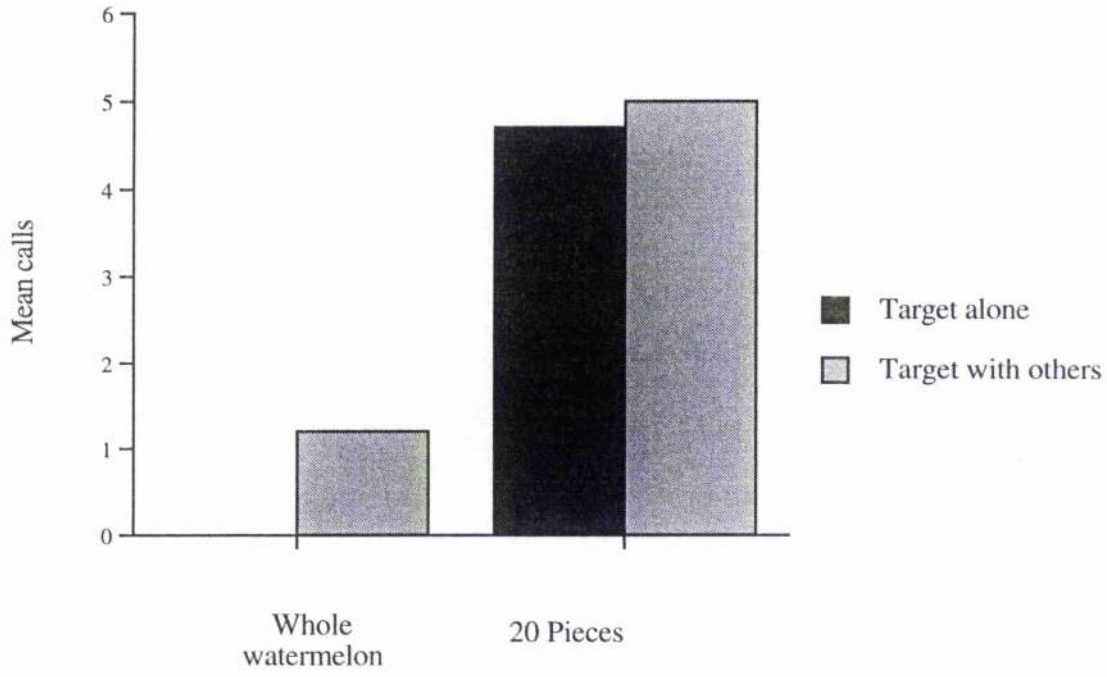

Figure 10.2. The effect of divisibility of food and social audience in the calling behaviour of targets

As in experiment 1, four different call types were given: *rough grunts*, *screams*, *squeaks* and *grunts* (see table 10.6.). However, the targets never gave *pant-hoots* when seeing the food. *Rough grunts* were the most common vocalization and always the first one to be given when other calls were produced. The number of *rough grunts* given was not significantly different in the two food conditions (Fisher Exact; p=0.24). The number of other calls per condition was not enough to test for the effect of food divisibility (all cases of *screams*, *squeaks* or *grunts* occurred when the 20 pieces of watermelon were thrown).

Table 10.5. also shows the total number of calls given by individuals of different ranks in different social contexts. Since there were no differences in the amount of calling of targets that were alone or with others, I lumped trials of both audiences and compared the total number of calls given by high-ranking or low-ranking males. A Mann-Whitney test showed that high-ranking males did not call more than low-ranking ones (W=96.5; p=0.53; adjusted for ties).

In a situation such as the one presented in this experiment, i.e. a male alone or with one other individual, finding food out of sight from the rest of the group, the male might be able to eat more food if he does not advertise his discovery to potential competitors. However, the fact that the target called or not when he saw the watermelon did not affect the amount of food he ate (Mann-Whitney; W=127.5; p=0.22; adjusted for ties)(see table 10.6).

As in experiment 1, the effect of the presence of an estrous female in male's calling behaviour was investigated. In 10 of the 21 trials a female (Lucy) was in estrous (see table 10.6.). The probability of a male calling in one trial was not affected by whether there was an estrous female in the group or not (Fisher Exact Probability test; p=0.05)(a female was in estrous in an equal number of trials in both conditions).

Food sharing behaviour

Ten cases of food sharing by the target were observed, one of active sharing of the whole watermelon and nine of passive relinquishment, distributed evenly between the two conditions, five in each (see table 10.7.). In nine of these cases of sharing the target shared the food with females and in two he shared it with males. When I considered all cases of sharing together (active and passive), the Fisher Exact Probability Test showed no significant difference in the amount of sharing between divisible and non-divisible foods (p=0.33).

Table 10.6. Experiment 2. Results on calling behaviour

Condition	Date	Target	Number of calls	Type of call	Pieces eaten by target	Females in estrous
	18/5/93	H-Rmale alone	0	none	7	Yes
	25/5/93	H-Rmale alone	13	rough grunt, squeak	4	No
	7/6/93	H-Rmale alone	5	squeak	15	Yes
	27/5/93	L-Rmale alone	2	squeak	6	No
	2/7/93	H-Rmale+female	11	rough grunt, squeak	13	No
20 pieces	26/5/93	L-Rmale+female	6	scream, squeak	6	No
	8/6/93	L-Rmale+other male	0	none	5	Yes
	15/6/93	L-Rmale+other male	3	rough grunt	12	Yes
	24/6/93	L-Rmale+other male	8	rough grunt, grunt, squeak	16	No
	20/5/93	L-Rmale+other male	4	rough grunt	8	Yes
	5/7/93	H-Rmale+other male	0	none	6	No
	7/7/93	H-Rmale+other male	6	squeak, scream	6	No
	3/6/93	H-Rmale alone	0	none	13	Yes
	25/6/93	H-Rmale alone	0	none	20	No
	9/6/93	L-Rmale alone	0	none	20	Yes
	10/6/93	L-Rmale alone	0	none	20	Yes
1 WM	21/6/93	L-Rmale+other male	0	none	13	No
	7/7/93	L-Rmale+other male	2	rough grunt	6	No
	8/7/93	L-Rmale+other male	4	rough grunt	5	No
	18/5/93	L-Rmale+female	0	none	20	Yes
	1/6/93	L-Rmale+female	0	none	2	Yes

Table 10.7. Experiment 2. Results on sharing behaviour and responses of other individuals

Condition	Target	Number of calls	Sharing	Females in estrous	Response of 2nd target*	Response of listeners**
	H-Rmale alone	0	Passive (with Lucy)	Yes	_	Call, present, fear grimace
	H-Rmale alone	5	No	Yes	_	Approach, grab food
	H-Rmale alone	13	Passive (with Lucy)	No	_	Call, grab food
	L-Rmale alone	2	No	No	_	Approach, grab food, fear grimace
	L-Rmale+female	6	No	No	Call, grab food	Approach, call
20 pieces	H-Rmale+female	11	No	No	Grab food	_
	L-Rmale+other	0	No	Yes	Grab food, scan	Approach, call
	L-Rmale+other	3	Passive (with Ricky)	Yes	Grab food	_
	L-Rmale+other	8	No	No	Grab food	Approach
	L-Rmale+other	4	No	Yes	Call, grab food	_
	H-Rmale+other	0	Passive (with Lucy)	No	Call, grab food	Grab food
	H-Rmale+other	6	Passive (with Lucy)	No	Present, feargrimace, grab food	Approach
	H-Rmale alone	0	Passive (Lucy+Emma) & active (with Emma)	Yes	_	Approach, grab food
	L-Rmale alone	0	No	Yes	_	_
	L-Rmale alone	0	No	Yes	_	_
	H-Rmale alone	0	No	No	_	_
1 WM	L-Rmale+other	2	Passive (with Lucy)	No	Call	Approach
	L-Rmale+other	4	Passive (Ricky+Lindsey)	No	Call	Approach, call
	L-Rmale+female	0	No	Yes	Follow target	_
	L-Rmale+female	0	No	Yes	Call, grab food	_
	L-Rmale+other	0	Passive (Lucy)	No	Beg for food	Approach, call

* Response of second target: the other individual accompanying the target.

** Response of listeners: individuals that heard the call from the inside or simply happened to go to the outdoor enclosure when the target was eating

In order to test if an individual who had previously called would be more willing to share afterwards the Fisher Exact was used. Individuals who had called upon seeing the food showed no significant difference in the amount of sharing compared to individuals who had not called (p=0.33). The probability of sharing was not affected by the presence or absence of the estrous female (Fisher Exact Probability Test; p=0.18).

In six of the 11 cases in which sharing took place (passive relinquishment) the discoverer shared the food with Lucy, who was in estrous in only 3 of these trials. The only case of active sharing occurred between a high-ranking male (Leo) and a female, Emma, and followed a similar pattern as the three cases described in experiment 1.

Responses of the individual accompanying the target

There were 13 trials in which the food was dropped and the target was accompanied by one other individual (in eight, the 20 pieces were dropped; in five, the whole watermelon). The response of this individual varied, it sometimes followed the target, called or grabbed food, and in one trial in which the target was a high ranking individual, it exhibited submissive behaviour towards him (presented its rear to the target and pulled a fear grimace towards him, before starting to grab some food). In two trials, both the individual accompanying the target and the main target (low ranking male) called and then scanned towards the indoor enclosure, where the rest of the group was, before starting to eat the food (see table 10.7.).

In the analysis of the responses of the individual accompanying the target the most important points to investigate were: whether there were differences in any of the responses in the two conditions the food was thrown, whether this individual behaved differently depending on the rank of the target, and whether there was a difference in its response depending on the fact that the target had called or not upon seeing the food (since this calling may warn the rest of the group in the indoor enclosure). The Fisher Exact test was used with those responses for which enough data were collected, i.e. call, grab food and act submissively (fear grimace or beg for food). The individual accompanying the target did not call more or act more submissively in trials in which the 20 pieces were dropped versus those in which the whole watermelon was dropped (p=0.40; p=0.27). However, the individual accompanying the target grabbed food in more trials in which 20 pieces were dropped than in trials in which the non-divisible watermelon was dropped (p=0.006)(see table 10.7.). There were no significant differences in the responses of the accompanying individual when the target was high or low ranking (call, p=0.26; grab

food, p=0.29; act submissively, p=0.41), nor when the target had called or not upon seeing the food (call, p=0.45; grab food, p=0.39; act submissively, p=0.27).

Responses of the listeners of the call

On the 13 occasions in which some individual in the indoor enclosure who had not seen the food drop heard the target calling or happened to go outside and discovered that there was food, its behaviour was always to approach the target/s, call and grab food. There were only two trials (one when the target was high-ranking and one when he was low-ranking) in which a single individual came out and found a male alone with the 20 pieces of watermelon. In these instances the possessor, a high ranking male in one trial and a female in the other, acted submissively towards him, presenting its rear and feargrimacing, before starting eating some of the food. In no instance did any chimpanzee behave aggressively (supplants or charges) towards target/s who were caught eating food and had not previously called.

As in the previous analysis above, a Fisher Exact test was used to investigate whether there were any differences in responses (approach, call and grab food) in the two conditions the food was thrown, whether the listeners of the call behaved differently depending on the rank of the target, and whether there was a difference in their response depending on the fact that the target had called or not upon seeing the food. There were no significant differences in the responses of listeners of the calls when the target was found eating divisible versus non-divisible food (approach, p=0.30; call, p=0.44; grab food, p=0.34). Nor were there any differences in the their responses when the target had called or not upon seeing the food (approach, p=0.5; call, p=0.32; grab food, p=0.41). The rank of the target did not influence the responses of the listeners of the call towards it (approach, p=0.06; call, p=0.30; grab food, p=0.08).

10.5. GENERAL DISCUSSION

In the last experiment described in this chapter chimpanzees were presented with divisible or less divisible food while they were in different social contexts. Male chimpanzees called more when finding a divisible preferred food (20 pieces of watermelon) than a less divisible food (whole watermelon). However, the males' calling was not influenced by the social audience they were with when seeing the food.

Listeners of the call did not respond differently (e.g. approach, call, supplant or display the discoverer/target) in trials when different food conditions were presented, with the exception of one of the responses examined. The individual accompanying the target grabbed food more often in trials in which the target found 20 pieces of watermelon than in those in which he found a whole one. This result makes sense considering the fact that there is more food to grab in a pile of 20 pieces of food than in a big chunk of food. An important aspect to consider if one wants to find out whether chimpanzees call more in the presence of particular individuals is how these specific individuals responded to calls. None of the behavioural responses examined differed in trials when the caller had or had not called.

If calling is an honest way of communicating to other group members that one has found food, then one would expect individuals who announce their discoveries to be more keen to share with others than individuals which have kept their discovery silent. Since I did not find any difference between callers and non-callers in their amount of sharing afterwards, I can only conclude that calling is performed for other reason than honest advertisement of willingness to share. Although most of the males' sharing was done with the female that was in estrous during the study (Lucy), suggesting that sharing behaviour may be dependent upon the subsequent benefits, i.e. preferential access to an estrous female, males did not call more when there was a female in estrous in the group.

The overall pattern of call use is consistent with the hypothesis put forward in the Hauser et al. (1993) paper, that *rough grunts* tend to be the first vocalization to be given when finding food (three different studies have shown this), providing the contextual referent that some palatable food is available. This idea was already suggested by Marler and Tenaza (1977), who pointed out that rough grunting may incorporate a message about the signaler's discovery of a favoured food, representing the most referential call in the chimpanzee's repertoire. Thus, *rough grunts* may be the 'food call' par excellence, whereas *pant-hoots*, *screams* and *squeaks* could provide information to others about the caller's level of arousal in the context of food. A possible explanation for the general lack of *pant-hoots* in my experiments could be that watermelon was not exciting or rare enough for this group of chimpanzees, specially if we consider that in the recording period before the experiments began, numerous and long choruses of *pant-hoots* were recorded in feeding and non-feeding contexts, from males and some females. However, before coming to a firm conclusion, acoustic analyses of all the calls recorded, specially of *rough grunts*, need to be done in the future together with cautious playback experiments in order to check if there are distinctive acoustic features in the calls (i.e. call rate) within particular food types or conditions.

A question that needs to be explained is why was there a food divisibility effect in the calling of chimpanzees alone or in pairs and there was no such an effect in the first experiment, when a whole group was present in the discovery moment. A possible explanation may be that the social context varied. In the first experiment the discoverer found a supply of food when the other group members where not far from him/her, actively foraging. However, in the second experiment the target/s found the food when no other individuals were present (the whole group was in the indoor cages), thus the chances of being caught eating a preferred food without having called were less. Of course, this applied equally when they found 20 pieces, but this may have been perceived as more in quantity than a whole watermelon and as more shareable, so the risk of ending up with nothing were smaller.

Chimpanzees in this study did not modify their amount of calling depending on which individuals were present. Although I cannot add new data to the existing evidence of an audience effect in wild chimpanzees (Mitani and Nishida 1993), chimpanzees did seem to be able to take into account the presence or absence of the group as a whole and the shareability of the food found, and according to this information decide whether to call or not. That is, they did not alter or suppress their calling if particular individuals were present (e.g a high ranking male or a female), but they did withheld their calling when they were completely on their own. In social species where individual recognition and memory of past interactions are well developed, withholding information provides an effective means by which animals can deceive one another without being detected, whereas active falsification will imply a larger risk in case of being caught. The calling that sometimes accompanies the discovery of a food source is a situation in which animals may deceptively manipulate information. In the wild, chimpanzees that come upon a large fruiting tree give loud *pant-hoots* that attract other individuals. However, sometimes they remain silent if only a little food is available (Wrangham 1975). Furthermore, studies in captive chimpanzees (Hauser and Wrangham 1987; Hauser et al. 1993) have shown that captive chimpanzees are relatively quiet when they discover small amounts of food, but call frequently when larger quantities of shareable food items are encountered. Evidence of withholding information about food can be found in other primate species and other animals (e.g. spider monkeys reducing their calling at small food sources, Chapman and Lefebvre 1990; toque macaques reducing their calling at food sources where the food is unripe or scarce, Dittus 1984; house sparrows suppressing their calls when finding non-divisible pieces of bread, Elgar 1986; and cockerels supressing their calls when finding food in the presence of another male, Marler, Dufty and Pickert 1986b). A recent study with captive pygmy chimpanzees suggested that they are able to suppress spontaneous vocalizations, thereby withholding information about food presence (Van Krunkelsven 1996).

In a considerable number of trials in both of my experiments the discoverers or targets did not call when finding food in either particular form (several pieces or the whole fruit). Hauser and Marler's (1993b) experiments with rhesus macaques in Cayo Santiago showed that silent discoverers who were detected by other group members received significantly more aggression than vocal discoverers. Results suggested that food-associated calls are 'honest' signals, reflecting food possession and that there might be a convention according to which animals who fail to signal, and are caught with food, are apparently punished. I found no evidence of a similar convention in chimpanzees. I observed a total of 17 cases in which a discoverer or target did not call and in six of these other chimpanzees caught the individual eating the food. In only two cases did they receive any form of aggression (aggressive displays), loosing all the food in one. In the second experiment, there were no cases in which a target individual who was caught eating food without previously calling received any form of aggression, but five of these were instances in which there was a second individual accompanying the target for whom the costs of announcing the food could have been larger than the benefits of keeping quiet and eating as much as the target allowed him/her.

I did not observe any case in this study of deception through falsifying information (e.g. by giving food calls when no food was found in order to attract the estrous female in the group). An explanation for the absence of deception through falsifying information may be the fact that these chimpanzees live in a stable group in which individuals recognize one another, remember past interactions and need some degree of cooperation, specially considering the reduced space of a captive environment. Perhaps other experiments in a different context to the feeding one (because of the large quantity of food these individuals get) will generate situations in which clear deceptive behaviours by falsifying information will emerge.

Chapter 11
Conclusions

As I draw several conclusions from the results found in this thesis, I will follow the order in which topics were presented in the main Introduction, referring to the spider monkeys' results first, and then integrating them with the chimpanzees' results.

In my study of spider monkeys' vocal communication I have concentrated in the function and meaning of two types of call, the *whinny* and the *bark*. I discovered that there are two functionally distinct *whinnies*; a locational *whinny* which functions as a position indicator, allowing spider monkeys to maintain vocal contact with each other; and a feeding *whinny* which functions to inform others about the discovery of food. However, what information do these calls communicate and to what extent can the feeding *whinny* be considered a referential or semantic call in the 'weakest sense' that I discussed in the Introduction chapter? Feeding *whinnies* seem to communicate information about environmental referents, while locational *whinnies* communicate information about social referents. However, none of the two have a high degree of stimulus specificity (or 'production specificity', as defined by Macedonia and Evans 1993). They may therefore occupy an intermediate position in a motivational-referential continuum (Marler et al. 1992). Since it is an established fact that no primate signal can be considered as completely motivational or completely referential, all have both components, the feeding *whinny* could be an example of one of the multidimensional models hypothesized by Marler et al.(1992). In this sense, this type of *whinny* will be a food call with a certain degree of ambiguity, but still function referentially. According to the model, food characteristics (e.g. amount of ripe fruit in a tree) and motivational state (e.g. high level of arousal) would interact to determine a *whinny*'s acoustic structure.

The other spider monkey call studied, the *bark*, functions as an alarm call to attract conspecifics to a site, maintain visual vigilance and warn kin of the presence of some danger. *Barks* may provide information about how close to the caller the predator (or any type of danger) is, but do not seem to convey information about predator type. The reason for this may be that the differentiation of predator classes in this species does not represent a significant advantage in reproductive success. As is the case with the *whinny*, this call does not have a high degree of production specificity, since it is given to a wide range of stimulus including some which are not even spider monkeys' predators (e.g. white-tail deer or crested guans). In this sense, the *bark* will be placed more towards a motivational end on the referential-motivational continuum.

In the case of chimpanzees, the only call I can draw any conclusions about is the *rough grunt*, since almost no *pant-hoots* were recorded in my experiments. The function of *rough grunts* in chimpanzees seems to be to indicate food availability, and they might be produced or suppressed depending on how shareable the food is and whether or not other individuals are nearby. The *rough grunt* fulfils the production specificity criterion, since it occurs predominantly when finding preferred food. In my experiments and in a previous study (Hauser et al. 1993) there is evidence that *rough grunts* communicate information not only about preferred food, but also about the divisibility of the food found. Chimpanzees called more often when finding divisible food than less divisible food. Although it is considered to be the most referential call in the chimpanzees' repertoire, no playback experiments or acoustic analyses have been performed on this call as yet.

A different issue reviewed in the Introduction concerned the deceptive use of vocal signals (e.g. food calls) by withholding them in situations in which the caller will obtain some benefits by doing so. There is evidence in both spider monkeys and chimpanzees of manipulation of information by suppressing food calls, apparently reducing feeding competition (Chapman and Lefebvre 1990; Wrangham 1975). However, experimental evidence has only been provided in chimpanzees, but not in spider monkeys, and the number of cases of deception by concealing calls recorded (see Byrne and Whiten's 1990 catalogue) is notably superior in chimpanzees. In the experiments described in the second part of my thesis, chimpanzees withheld vocalizations when they were completely on their own, in a situation in which calling would have increased feeding competition and risked the loss of some food. On the other hand I found no evidence in this group of captive chimpanzees of the so called 'audience effect', e.g. adult males calling more frequently when alliance partners or associates were nearby (Mitani and Nishida 1993). The rank or sex of the individual nearby the caller did not affect the caller's vocal behaviour.

Several of the similarities in spider monkeys and chimpanzees' vocal communication described in the Introduction have been corroborated in this thesis. Both species use food calls (with different levels of referentiality) to advertise the discovery of food; both species use loud calls during inter-community encounters; both species show evidence of individual vocal differences in some of their calls. In the case of spider monkeys, there are individual differences in their *whinnies*; although they do not seem to vocally discriminate between individuals of a different community and familiar individuals by their *whinny* calls. In the case of chimpanzees, individual differences exist in their *pant-hoots*. However playback experiments are necessary to demonstrate vocal recognition. Both species have a graded and complex vocal system in which calls intergrade into one another as a function of changes in motivational state. The complexity of their vocal behaviour

could be associated with the unstable subgroups associations which characterizes their fission-fusion social organization.

In my opinion, future comparative studies should concentrate on investigating socio-ecological similarities and differences which may have caused the corresponding similarities and differences in the vocal communication of spider monkeys and chimpanzees. A possible example concentrating on the similarities, could be to correlate a social factor, such as behaviour during inter-community encounters, with a specific vocal trait which could be an adaptation to that particular situation, e.g. use of loud calls to avoid physical and energetically expensive confrontations. An example concentrating on the differences, could be to correlate different lifestyles and their subsequent environmental constraints with variations in the species' call structure which may have evolved to improve sound localization.

APPENDIXES

Appendix I

Catalogue of spider monkeys' (*Ateles geoffroyi*) vocalizations

(from Eisenberg and Kuehn 1966; Eisenberg 1976)

Call type	Function	Context	Response of receivers	Acoustic features	Associated expression
WHINNY	Position indicator that accompanies feeding and may serve to indicate food availability;promotes assembly	Often given when an adult first enters a fruit tree or when subgroups join. Both by males and females.	Approach, join, give whinnies	Highly modulated, long duration (1.5-2.5 sec) repetitive, dominant frequency high clear tone, freq.range1.0-5.2 Khz	Lips closed
TEE TEE	Position indicator, greeting call	Given at the approach of a troop member or familiar individual	Approach, join, give whinny	Short duration (0.5 sec),not repetitive dominant frequency high, clear tone freq.range 1.2-5Khz	Lips closed, chin-up
SQUEAK (trills, twitters)	Appeasement and contact promoting	Given by an approaching animal, often after it has been repulsed	Assume attentive posture look at, turn and "assist"	Short duration (0.35 sec), repetitive, dominant frequency high, clear tone, freq.range(2.9-3.1)	Lips closed
OOK-OOK	Indicator of arousal level; may function as an invitation to play	Accompanies grapling, or mock fighting; at low intensity accompanies sexual behaviour	Head-shake, give ook-ook	Short duration, grunting sound repeated rapidly Dominant frequency low, blurred harmonics freq. range (2-3 Khz)	Mouth may be open with pursed lips; no tooth exposure; head often shaken horizontally
BARK	Position indicator, promotes assembly; can serve as a warning signal, part of mobbing	Response to an alien stimulus serves to alert group and focuss attention on the responding animal	Branch shaking, leaps or give barks as well	Short duration,repetitive, dominance freq.low blurred harmonics, freq.range(2,2-2,8 Khz)	Little or no tooth exposure mouth open; pilo-erection
GROWL (roar)	Indicates a hostile approach	Accompanies threat or attack behaviour	Move away	Short duration (0.5 sec) with a blurred harmonic structure, non repetitive, dominant freq. low, freq.range(0.2-2.6Khz)	Mouth may be open; lip retraction may not be pronounced; direct stare
LONG CALL	Position indicator, may promote assembly', facilitates subgroups mergers	When brachiating, troop assembly during intergroup encounters	Approach, join, give whinny	Relatively harmonic in tonal structure durat. more than 2sec., loud and often repeated.	Open mouth with little tooth exposure

Appendix II

DESCRIPTION OF CATEGORIES

(Following Fedigan and Baxter 1984; van Roosmalen and Klein 1988)

1. Register (10" interval, point sample): the behaviour is registered instantaneously.

LOCATION of the focal in a map of the study area. At the end of observation session draw a map of the route.

FORAGE (F): search for a food item by visual or manual inspection (in tree holes, picking through leaves, etc.).

MOVE (M): locomote in any mode (climb, brachiate, walk)

DRINK (D): ingest water from any source (e.g. water tree holes, droplets of leaves).

EAT (E): ingest or masticate a food item: bark, flowers (a flower or a bud), fruit (seeds, pods, nuts), mature leaves, young leaves, stems, roots, minerals and soil, insects. Write the food item in the context column.

REST (R): the focal is not locomoting and is not engage in any of the activities named above.

COMPOSITION-SIZE OF SUBGROUP: approximate size of subgroup, number of individuals who seem to be foraging, moving or eating together. Under column SZ (size).

GIVE GROOM (+ GR): pick through fur of a second with hands and/or mouth. The receiver of grooming is written in the context column.

RECEIVE GROOM (- GR): another animal picks through the fur of the focal with hands and/or mouth. The groomer is written in the context column.

VIGILANCE STATE

0. Relaxed: not vigilant, sleeping, resting or moving without scaning.

1. Vigilant: scaning at a slow rate or at a rapid rate.

2. Socially aroused: involved in a social interaction (e.g. grooming).

3. Aggressive: involve in any aggressive interaction, threatening body postures or vocalizations.

4. Frightened: submissive facial expressions and body postures by an animal being threatened or chased.

2. Continuous recording:

2.1. VOCALIZATIONS:

* Type of call.
* Time of occurrence is written for each vocalization (if the caller cannot be identified, register the size of the subgroup it is in, the identification of any other individual nearby, and the distance between them). Try to determine if there is a time of day or place (sleeping trees) when spider monkeys are more vocal.
* Context of the vocalization: events surrounding the emission of the vocalization (entering a fruiting tree, joining a group), other vocalizations given, other events (interspecific encounter, human observer nearby, predator).
* Response of the receivers of the call: approach the caller, call as well, look in the direction of the caller.
* Identified individuals in hearing distance.

2.2. Aggressive behaviours: register all identifiable adults within 5 meters. Record the time at the start of the interaction sequence and write subsequent behaviours on following lines; when it is possible, write the times of each subsequent behaviour.

ATTACK: aggression involving physical contact, including slaping, hiting and occuring in the context of social excitement, when many individuals are vocalizing loudly and locomoting rapidly (Fedigan & Baxter 1984). According to these authors only males performed this behaviour.
CHASE: one animal runs after a second and the second runs away from the first.
SUPPLANT: A approaches B to within one meter and B leaves, abandoning its resource(s) (e.g. access to drinking source, proximity to a third animal). The resource is written in the context column.
DISPLACE: A approaches to within one meter of B and B moves away, leaving A to take over B's spot; there is no recognizable resource at the spot left by B.
MOBBING DISPLAY (species-specific): a first description of this behaviour by Eisenberg 1976 was: performed by adult males against intruders. The sequence involves quadrupedal run, tail held up, pilo-erection, rapide brachiation after the run toward the object, swinging towards it grasping nearby branches and maybe shaking them. Open mouth with full tooth exposure. Fedigan & Baxter 1984 defined it as a territorial display: a higly ritualized arboreal display involving several individuals leaping, branch shaking, mounting each other and mobbing together while giving loud vocalizations (long calls by

Eisenberg 1976). Frequently performed near the tops of tall trees, accompanied by intensive vigilance and responded to by similar behaviour from another group of spider monkeys.

BRANCH SHAKE: animal shakes a tree branch (or similar object) with a rithmic movement, jumping upon and down flexing and extending all four limbs while grabing a fixed object with the tail (Eisenberg & Kuehn 1966). There may not be any individual receiver of this behaviour but maybe another stimulus, such as a neighboring group.

HEAD SHAKE: while looking directly at another individual the head is moved back and forth in the horizontal plane. It accompanies an initial contact or a renewed contact where the animal is ambivalent in its approach. It may also occur when a contact situation is about to break up as a result of mixed agonistic tendencies on the part of the other animal. It correlates with the facial expression open mouth with canines unexposed (Eisenberg & Kuehn 1966).

HAIR BRISTLE: erection of the hair.

GRIMACE: a facial expression involving partial opening and retracting of the corners of the mouth combined with raising the upper lip, thus exposing the teeth. This expression seems to induce moving away in an approaching animal, and it is often reinforced by a slap, rush, or bite (Eisenbers & Kuehn 1966)

BITE/HIT: according to Eisenberg 1976 'sudden aggression may be displayed when an animal slaps another. Rarely does biting occur, but when it does, it is often swift with the bitten animal fleeing immediately, screaming and remaining as far away from the attacking animal...'

2.3. Submissive behaviours:

AVOID: an animal moves away from a second as the second one moves towards, but not within one meter of the first.

MOVE/RUN/WALK AWAY: an animal moves, runs or walks away a second as the second animal directs any kind of aggression towards the first.

2.4. Affinitive or contact-promoting behaviours:

SIT IN CONTACT: an animal sits besides another.

EMBRACE: may be mutual or performed by one member of an interacting pair. It involves placing the arms around the body of the second animal (Eisenberg & Kuehn 1966). Often accompanied by the slow whinny.

PECTORAL SNIFF (species-specific): mutual placing of the mouth and/or nose in the pectoral region (or axilla) where scent glands occur. Occurs only during an embrace (Eisenberg & Kuehn 1966). Described by Klein (1972) as a greeting signal. When males

of the same social group meet each other after a period of separation, they engage in this very ritualized olfactory exchange.

PURSED LIPS: a facial expression involving an extension of the lips. The teeth are virtually invisible. It occurs during contact-promoting behaviour (Eisenberg & Kuehn 1966).

2.5.Sexual-olfatory:

GRAPPLING: a complex pattern accompanied by the ook ook vocalization. Involves elements of the embrace: pushing away, pulling toward, mock biting and slaping. Ook ook sounds may grade into roars and the bout may end in a chase. Certain elements of sexual behaviour including mutual manipulation of the genitalia with the mouth, hands or feet also occur (Eisenber & Kuehn 1966). However it can also occur in non-sexual contexts and it is most frequently shown by juvenile and subadult males. According to Eisenberg 1976 the exact motivation of grappling is difficult to evaluate. Some times it seems to have aggressive connotations, while at other times it seems to have some sexual significance. It should not be considered as a necessary prelude to sexual behaviour.

GENITAL INSPECT; FINGER SNIFF; BRANCH SNIFF: a male would touch the female's clitoris and then sniff his fingers; he may also sniff the branch upon she was sat, marked or urinated.

2.6.Other behaviours:

PRESENT FROM GROOM: the whole body or a part of it (the back) is exposed to a second. The posture can be sitting, lying down, or standing quadrupedally.

APPROACH: an animal moves towards another by any mode of locomotion. Generally the approaching animal looks directly at the other. Record only the approaches as part of behaviour sequences of interest since they may be so common.

PRESENT FOR SEXUAL MOUNT: presentation of the genitals on the part of the female as one of the element described by Eisenberg 1976 of *Ateles* sexual behaviour. In all copulations he observed the female played an active role in approaching the male, touching and eventually sitting in his lap. The male also may be active in initiating the copulatory position by extending toward her with his hind legs and attemping to lock them around her torso.

APPENDIX III

SPONTANEOUS ALARM CALLING BOUTS OF SPIDER MONKEYS AT SANTA ROSA

(FOCAL ANIMAL SAMPLING)

BOUT #	DATE	SUBGROUP SIZE	STIMULUS ELICITING CALLS	TYPE ALARM CALL	DURATION	OTHER BEHAVIOURS	DOES CALLING ATTRACT OTHERS?	WHO STARTS CALLING?	CONTEXT
1	28/11/93	7	Big bird flying over heads	Hiccup bark	?	Scann towards birds	No	Juvenile	Feeding
2	7/12/93	7	Unidentified	Barks	?	Branch-shake Flee from site	No	Adult female	Feeding
3	2/1/94	1	Observer (Unhabituated female)	Bark	?	Flee from site	No	Adult female	Moving
4	2/1/94	4	Observer	Barks	3 min.	Mob, branch-shake throw twigs	No	An adult and juvenile males	Feeding
5	6/1/94	8	Crested goan calling alerted by observer	Barks	?	Flee from site	No	?	Moving
6	6/1/94	8	Observer (Unhabituated indiv.)	Hiccup barks	20 min.	Mob towards observer throw twigs	Yes (two adult males join the mobbing against observer)	Two juvenile females	Resting
7	22/2/94	2	Large pigeon alerted flying from ground	Barks	8 min.	Flee from site	No	Both females	Moving
8	22/4/94	2	Agouti alerted by observers	Barks	10 min.	Branch-shake towards observers	No	Adult female	Moving
9	22/4/94	2	White-tail deer alarm calling alerted by observers	Barks	1 min.	_	No	Adult female	Feeding
10	6/5/94	2	Coyote	Barks	40 min.	Branch-shake, head-shake scann	No	Both , the adult female and the juvenile male	Moving
11	4/1/94	2	Raptor flying over (unidentified species)	Barks	2 sec.	Look towards sky scann	Yes, other individuals nearby call as well	Subadult female	Feeding

BOUT #	DATE	SUBGROUP SIZE	STIMULUS ELICITING CALLS	TYPE ALARM CALL	DURATION	OTHER BEHAVIOURS	DOES CALLING ATTRACT OTHERS?	WHO STARTS CALLING?	CONTEXT
12	1/3/94	5	Unidentified	Barks	1 min.	Scann alert towards the ground	Other individuals join the alarm calling	Subadult male	Moving
13	11/3/94	2	Observers	Barks	10 min.	Scann towards observers	No	Adult female	Resting
14	30/4/94	2	White-tail deer alarmed	Barks	5 sec.	Scann	No	Adult female	Resting
15	21/2/94	3	Observers	Barks	?	Look towards observers	No	Adult female	Moving
16	1/3/94	3	Unidentified	Barks	30 min.	Scann towards ground alert	No	Two adult females	Resting
17	6/4/94	3	Pigeon flying from ground	Barks	4 min.	Scann towards sky	No	Adult female	Resting
18	23/4/94	2	Crested goan alarm calling	Barks	2.50min	Scann alert	No	Two subadult females	Moving
19	25/4/94	1	Observer	Barks	12 min.	Scann alert	No	Adult female	Moving
20	6/5/94	2	Large hawk perched crying	Hiccup barks	14 min.	Scann towards hawk	Yes, other congregate at same site and give barks and whinnies	Adult female	Feeding
21	29/8/94	2	Unidentified	Barks	15 min.	Scann towards ground	No	Subadult male	Resting
22	5/10/94	3	Group o storks flying over their heads	Hiccup barks	52 sec.	Look up, scann	Other individuals alarm call as well	Subadult female	Feeding
23	13/10/94	2	Unidentified	Barks	2 min.	Scann	Suadult female gives barks as well	Adult female	Feeding
24	27/10/94	6	Large group of Turkey vultures feeding on carcass	Hiccup barks	?	Scann towards vultures	No	Juvenile male	Moving

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